SHOUT
SHARE
IT

THE JOURNAL
OF
ANIMAL BEHAVIOR

VOLUME 4, 1914

EDITORIAL BOARD

Madison Bentley
University of Illinois

Harvey A. Carr
The University of Chicago
Editor of Reviews

Gilbert V. Hamilton
Montecito, California

Samuel J. Holmes
The University of California

Walter S. Hunter
The University of Texas

Herbert S. Jennings
The Johns Hopkins University

Edward L. Thorndike
Teachers College, Columbia University

Margaret F. Washburn
Vassar College

John B. Watson
The Johns Hopkins University

William M. Wheeler
Harvard University

Robert M. Yerkes, Harvard University
Managing Editor

Published Bi-monthly
at Cambridge, Boston, Mass.
HENRY HOLT AND COMPANY
34 West 33d Street, New York
G. E. STECHERT & CO., London, Paris and Leipzig Foreign Agents

Entered as second-class matter March 7, 1911 at the post-office at Cambridge, Boston
Massachusetts, under the act of March 3, 1879.

CONTENTS OF VOLUME 4, 1914

NUMBER 1, JANUARY-FEBRUARY

PAGES

Victor E. Shelford and **W. C. Allee.** Rapid modification of the behavior of fishes by contact with modified water. 1–30

Victor E. Shelford. Modification of the behavior of land animals by contact with air of high evaporating power. 31–49

Robert M. Yerkes and **Chester E. Kellogg.** A graphic method of recording maze-reactions.................. 50–55

John B. Watson. A circular maze with camera lucida attachment 56–59

Helen B. Hubbert. Time versus distance in learning.... 60–69

W. T. Shepherd. On sound discrimination by cats...... 70–75

H. M. Johnson. A note on the supposed olfactory hunting-responses of the dog.......................... 76–78

NUMBER 2, MARCH-APRIL

Eupha Foley Tugman. Light discrimination in the English sparrow 79–109

Harry Beal Torrey and **Grace P. Hays.** The rôle of random movements in the orientation of *Porcellio scaber* to light 110–120

Wallace Craig. Male doves reared in isolation.......... 121–133

H. M. Johnson. Hunter on the question of form-perception in animals 134–135

Harold C. Bingham. A definition of form..............136–141

Sergius Morgulis. The auditory reactions of the dog studied by the Pawlow Method....................... 142–145

NUMBER 3, MAY-JUNE

John H. Lovell. Conspicuous flowers rarely visited by insects 147–175

Robert M. Yerkes. The Harvard Laboratory of Animal Psychology and the Franklin Field Station........... 176–184

Charles A. Coburn. The behavior of the crow, *Corvus Americanus, Aud* 185–201

W. C. Allee and **Shiro Tashiro.** Some relations between rheotaxis and the rate of carbon dioxide production of isopods 202–214

W. S. Hunter. The auditory sensitivity of the white rat. 215–222

5112

PAGES

Henry H. P. Severin and Harry C. Severin. Behavior of the Mediterranean fruit fly (*Ceratitis Capitata Wied.*) towards kerosene 223–227

NUMBER 4, JULY-AUGUST

Lee Raymond Dice. The factors determining the vertical movements of Daphnia 229–265

Raymond Pearl. Studies on the physiology of reproduction in the domestic fowl. VII. Data regarding the brooding instinct in its relation to egg production..... 266–288

Osv. Polimanti. On the thele-perception of sex in silkworm moths 289–292

K. S. Lashley. A note on the persistence of an instinct. 293–294

NUMBER 5, SEPTEMBER-OCTOBER

G. V. Hamilton. A study of sexual tendencies in monkeys and baboons 295–318

H. M. Johnson. Visual pattern-discrimination in the vertebrates—I. Problems and Methods.............. 319–339

H. M. Johnson. Visual pattern-discrimination in the vertebrates—II. Comparative visual acuity in the dog, the monkey, and the chick.......................... 340–361

Sergius Morgulis. Pawlow's theory of the function of the central nervous system and a digest of some of the more recent contributions to this subject from Pawlow's laboratory 362–379

R. P. Cowles. The influence of white and black walls on the direction of locomotion of the starfish........... 380–382

NUMBER 6, NOVEMBER-DECEMBER

S. J. Holmes. Literature for 1913 on the behavior of the lower invertebrates 383–393

C. H. Turner. Literature for 1913 on the behavior of spiders and insects other than ants.................. 394–413

Stella B. Vincent. Literature for 1913 on the behavior of vertebrates 414–438

Walter S. Hunter. Pycraft on the infancy and courtship of animals 439–441

Walter S. Hunter. H. Volkelt's "Über Die Vorstellungen der Tiere".................................. 442–445

Subject and Author Index

VOLUME 4

Original contributions are marked by an asterisk (*)

*Allee, W. C. Behavior of fishes, 1;
*rheotaxis in isopods, 202;
rheotaxis in isopods, 383, 391, 396.
*Animal Psychology, laboratories for, 176.
Amoeba, reactions to food, 388.
Amphibians, literature on, 416, 423
Annelids, reactions of, 385.
Assagioli, R. Thinking horses, 436.
Association, literature on, 407.
*Audition, see hearing.
Austen, E. E. Fly and health, 406, 409.

Babák, E. Color vision in frogs, 417, 436.
*Baboons, sex tendencies in, 295.
Bailey, V. Life zones, 405, 409.
Baldasseroni, V. Animal intelligence, 436.
Balss, H. Chemical sensitivity in crustaceans, 383, 391.
Bancroft, F. W. Heliotropism in Euglena, 383, 391.
Barber, H. S. Life-history of beetles, 409.
Barrows, W. B. Instincts of bittern, 427, 436.
Baunacke, W. Function of the statocyst, 384, 391.
Bee, color vision in, 397.
Beetle, behavior of, 400.
Bénard, G. Behavior of beetles, 400, 407, 409;
acrobatic feats of insects, 407, 409.
Bergtold, W. H. Behavior of house finch, 427, 436.
Biddle, E. Hibernation of butterfly, 404, 409.
*Bingham, H. C. Definition of form, 136;
visual perception in chick, 419, 436.
Bird, H. Habits of Oligia, 406, 409.
Bird, literature on, 419, 422.
Bishopp, F. C. Biology of tick, 402, 404, 406, 409.
Bloclock, B. Insects and disease, 406, 409.
Bohn, G. Memory in lower organisms, 384, 391.
Brauns, H. Behavior of aphids, 406, 409.
Breed, F. S. Development of instinct, 426, 438.
Brierley, W. B. Life history of *Leptosphaeria*, 409.
Brocher, F. Respiration in insects, 409.
Browne, F. B. Life history of beetle, 409.
Brues, C. T. Distribution of stable flies, 405, 406, 409.
Brundin, M. Light reactions of amphipods, 384, 391.
Brunelli, G. Behavior of hermit crabs, 384, 391.
Buddenrock, W. v. Function of the statocyst, 385, 391.
Burrell, A. C. The giant midge, 406, 410.
Buttel-Reepen, v. Thinking horses, 436.
Buttrick, P. L. Breeding habits of mosquitoes, 399, 410.

*Camera lucida, for maze, 56.
Car, L. Locomotion of infusoria, 385, 391.
*Cat, hearing in, 70;
*instincts of, 293;
learning in, 428.
Chaine, J. Termites, 410.
Champion, G. C., Behavior of scirtes, 406, 410.
Chapman, T. A. Behavior of *Agriades*, 406, 410.
*Chartometer, for maze, 58.
Chemical sense, literature on, 423.
Chemotropism, literature on, 394.
*Chick, visual acuity in, 340.
Chubb, E. C. Habits of spiders, 403, 410.
Claparède, E. Trained horses, 434, 436.
Claude, D. Jumping spiders, 405, 410.
Clementi, A. Functions of the nervous system of diplopods, 385, 392.

Coad, B. R. Habits of mosquito, 399, 410.
*Coburn, C. A. The behavior of the crow, 185.
Cockle, J. W. Behavior of *Bombus*, 410.
Coelenterates, modifiability in, 387.
Cockerell, T. D. A. Behavior of hemiptera, 405, 410.
Cole, L. J. Locomotion in the starfish, 385, 392.
Cole, L. W. Behavior of raccoons, 415.
Collinge, W. E. Behavior of Collembola, 406, 410.
Comstock, J. H. Spider book, 404;
silk of spiders, 406, 410.
Cooke, W. W. Bird migration, 428, 436.
Copeland, M. Olfactory reactions, of fish, 423, 436;
of newt, 423, 436.
Copepods, the behavior of, 386.
*Courtship of animals, 439.
*Cowles, R. P. Behavior of starfish, 380;
habits of crustacea, 385, 392.
Crab, behavior of, 384.
*Craig, W. Behavior of doves, 121;
stimulation of egg laying, 427, 436.
Cros, A. Behavior of Hymenoptera, 406, 410.
*Crow, behavior of, 185.
Crustacea, habits of, 385, 390;
vision in, 388, 392;
acquired color response in, 390;
functions of antenna, 390.

*Daphnia, movements of, 229;
color responses of, 386.
Davis, J. J. Life cycle of *Lachnosterna*, 410.
*Dice, L. R. Movements of *daphnia*, 229.
Disease, in relation to insects, 406.
*Distance records for maze, 60.
Doane, R. W. Behavior of beetle, 402, 410;
insects and disease, 410.
*Dog, olfactory responses of, 76;
*auditory reactions of, 142;
*visual acuity in, 340;
learning in, 428.
*Doves, behavior of, 121.
Dubois, R. Reactions of Echinoderms to light, 392.
Dutt, G. R. Life history of Hymenoptera, 410.

Ecology, literature on, 405.
Ely, C. R. Feeding habits of *Cleonus*, 402, 410.
Emotions, literature on, 398.
Erhard, H. Color responses of *daphnia*, 386, 392.
Ettinger, M. Thinking horses, 436.
Ewing, H. E. Hibernation of lady bug, 404, 405, 410.

Fabre, J. H. Social life of insects, 399;
habits of spiders, 403, 405, 410.
Fasten, N. The behavior of Copepods, 386, 392.
*Field Station for animal behavior, 176.
*Fish, behavior of, 1;
literature on, 417.
Fiske, W. F. Behavior of *Glossina*, 406, 410.
*Flowers, visited by insects, 147.
Folbort, G. V. Inhibitory conditioned reflexes, 377.
*Form perception, in animals, 134, 136.
Franz, S. I. Right and left handedness in monkey, 425, 436.
Franz, V. The behavior of snails, 386, 392;
the value of phototaxis, 386, 392.
Frideman, S. S. Further contributions to the physiology of differentiation of external stimuli, 376.
Frisch, K. v. Color responses of crustacea, 386, 392;
color vision in insects, 397, 410;
color vision in fishes, 417, 436.
Frölich, F. W. Light and color vision in Octopus, 387, 392.
Frost, C. A. Habits of Diptera, 403, 410.
Frohawk, F. W. Life history of *Argynnis*, 406, 410.
*Fruit fly, behavior of, 223.
Fulton, B. B. Habits of crickets, 399, 412.

Gee, W. The behavior of leeches, 387, 392;
modifiability in the sea anemone, 387, 392.
Geotaxis, in *daphnia*, 229 .
Geotropism, literature on, 394.
Gerhardt, U. Sex behavior of crickets, 398, 410.
Gillette, C. P. Behavior of *populus*, 402, 410.

Girault, A. A. Habits of insects, 405, 410;
letisimulation of beetle, 407, 410.
Green, E. E. Humming of midges, 407, 411.
Gregarines, movements of, 385.
Gregg, F. M. Behavior of raccoons, 415, 436.
Guyenot, E. Behavior of *Drosophila*, 406, 411.

Habits, of crustacea, 385, 390;
breeding of Nereis, 388;
literature on, 425.
Hadwen, S. Tick paralysis, 406, 411.
Haggerty, M. E. Behavior of apes, 425, 437.
*Hamilton, G. V. Sexual tendencies in monkeys, 295.
Haenel, H. Thinking horses, 431, 437.
Harte, C. R. Flight of moth, 405, 411.
Hartman, C. Habits of bee, 400, 411;
habits of wasp, 407, 411.
*Harvard Laboratory of Animal Psychology, 176.
*Hays, G. P. Orientation of *Porcellio*, 110.
*Hearing, in cats, 70;
*in the dog, 142;
*in the white rat, 216;
literature on, 421.
Heinrich, R. Light reactions of insects, 394, 411.
*Hen, brooding instinct of, 266.
Hentschell, H. Aquaria for insects, 408, 411.
Heredity, of savageness and wildness, 425.
Hess, C. The color sense of animals, 388, 392;
vision of amphibians, 417, 437.
Herms. Transmission of poliomyelitis, 406, 412.
Herrick, G. W. Scale insects, 406, 411.
Hibernation, literature on, 404.
Hodge, C. F. Movements of flies, 405, 411.
*Holmes, S. J. Literature on behavior of invertebrates, 383;
light reactions of dermestidae, 394, 411;
orientation to light, 395, 411.
Homing, literature on, 407.
Horse, performance of trained, 431, 432.
*Hubbert, H. B. Time versus distance, 60.
*Hunter, W. S. Hearing in white rat, 215;
form perception, 397, 411;
delayed reactions, 435, 437;
*on infancy and courtship, 439;
*ideas in animals, 442.

*Ideas, in animals, 442.
Imitation, in parrot, 422.
Imms, A. D. Behavior of Indian insects, 411.
*Infancy, of animals, 439.
Infusoria, locomotion of, 385.
*Insects, in relation to flowers, 147;
*perception of sex in, 289;
light reactions of, 394;
*literature on, 394;
acrobatic feats of, 407.
*Instinct, of male doves, 121;
*brooding, 266;
*of silk worms, 289;
*persistence of, in cats, 293;
*of monkeys, 295;
methods of studying, 393;
mating literature on, 398;
maternal, 399;
nest-building 399;
defensive, 402;
procuring, 402;
literature on, 406, 425;
development of, 426;
*social, 439.
*Invertebrates, literature on, 383;
color sense of, 388.
*Isopods, rheotaxis in, 202.

Jennings. Insects and pellagra, 406, 411.
Jerofeeva, M. N. Electrical irritation of the skin of the dog, 378.
*Johnson, H. M. Smell, in the dog, 76;
*form perception in animals, 134;
*visual pattern discrimination, 319;
*visual acuity in animals, 340;
audition in dogs, 415, 421, 437.
Just, E. E. Breeding habits of Nereis, 388, 392.

Katz, D. Vision of night birds, 420, 437.
Kehschkowsky, K. Reactions of vermes to electricity, 388, 392.
*Kellogg, C. E. Graphic method for maze, 50.
Kepner, W. A. Reactions of *Amoeba* to food, 388, 392.
King, W. V. Biology of tick, 402, 404, 406, 409.

Klein, F. Behavior of *Chrysomela*, 411.
Knab, F. "Forest Malaria," 406, 411.
Kawlbersz, G. J. v. Reactions of isopods, 388, 392.
Krall, K. Trained horses, 432, 437.
Kupelweiser, H. Color responses of crustacea, 386, 392.

*Labyrinth, see maze.
Ladd-Franklin, C. Color vision in bees, 397, 411.
*Lashley, K. S. Persistence of an instinct, 293;
  imitation in parrot, 422, 437;
  development of young monkey, 425, 437.
*Learning, time and distance in, 60;
  literature on, 428.
Leech, modifiability in, 387.
Leplat, G. The eye of birds, 421, 437.
Letisimulation, literature on, 407.
*Light, orientation of *Porcellio* to, 110;
  *reactions to, of starfish, 380;
  reactions to, 384, 389;
  reactions to, in crustacea, 390;
  response to, by snails, 391;
  orientation to, 395.
Lillie, F. R. Breeding habits of Nereis, 388, 392.
Linstow. Diet of caterpillars, 402, 411.
*Literature for 1913, on invertebrates, 383;
  *on spiders and insects, 394;
  *on behavior of vertebrates, 414.
Locomotion, literature on, 405.
*Lovell, J. H. Flowers and insects, 147;
  a vernal bee, 411.
Lutz, A. Forest Malaria, 411.

MacCurdy. Reactions of starfish to light, 389, 392.
MacKenzie, W. Thinking horses, 431, 437.
Mammals, literature on, 414.
Mangin, M. Thinking horses, 437.
Mangold, E. Animal hypnotism, 428, 436.
Mansion, J. Insects living in formol, 411.
Mathews, A. Habits of *Gammarus*, 390, 393.
Matula, J. Functions of antenna of lobster, 390, 393.
*Maze, graphic method for, 50;
  *circular, with camera lucida, 56;
  *time and distance records for, 60.
McGraw, K. W. Orientation to light, 395, 411.
McIntyre, J. L. The rôle of memory, 431, 437.
McPheeters, C. A. Behavior of raccoons, 415, 436.
Meijere, J. C. A. Habits of Orthoptera, 406, 411.
Memory, in lower organisms, 384;
  literature on, 407, 428.
Menegaux, M. A. Educated horses, 437.
Metalnikow, S. Choice of food by paramoecia, 389, 392.
*Methods of studying vision, 340.
Migration, literature on, 405.
Mitzmain, M. B. Insects and disease, 406, 411.
*Modifiability, in fishes, 1;
  *in land animals, 31;
  in coelenterates, 397;
  in leeches, 387.
Mollusca, habits of, 389, 390.
*Monkey, sex tendency in, 295;
  *visual acuity in, 340;
  development of, 425.
Moore, A. R. Phototropism of *Diaptomus*, 389, 392.
Morgan, A. C. Behavior of beetles, 407, 411.
Morgan, A. H. Behavior of May-flies, 398, 402, 411.
*Morgulis, S. Reactions of the dog, 142;
  *Pawlow's theory of function of nervous system, 362.
Morse, E. S. Habits of *solenomya*, 389, 392.
Mosquito, behavior of, 395.
Movements, Brownian, 390.
Mrazek, A. Locomotion of *branchipus*, 389, 392.

Newell, W. The rice weevil, 398, 402, 411;
  letisimulation of weevil, 407, 411.
Nichols, M. L. Habits of bee, 400, 412;
  homing of bees, 407, 412.
Niewenglowski, G. H. Transmission of malaria, 406, 412.

Octopus, vision in, 387.
*Olfaction, see smell, 76.
*Orientation, of Porcellio, 110.
Orton, J. H. Natural history of limpet, 390, 392.
O'Shea, M. V. Educated horses, 437.

Paramoecium, choice of food by, 389.
Parker, G. H. Chemical sense of vertebrates, 423, 437;
  hearing in fishes, 424, 437.
Parrott, R. J. Habits of crickets, 399, 412.
*Pawlow, The Method of, 142.
  *theory of function of nervous system, 362.
*Pearl, R. The brooding instinct, 266.
Pearse, A. S. Habits of crustacea, 390, 393.
Phillips, J. E. Bird migration, 427, 437.
*Phototaxis, in daphnia, 229;
  its significance, 386.
Pictet, A. Hibernation of moth, 404, 412.
Plate, L. Thinking horses, 437.
Plessner, H. Reactions of the starfish, 390, 393.
*Polimanti, O. Behavior of silkworm moths, 289.
Popovivi-Baznosanu, A. Behavior of spiders, 406, 412.
Porcupine, behavior of, 429.
Protozoa, movements of, 390.
Przibram, H. Functions of antenna of lobster, 390, 393.
Przibram, K. Movements of protozoa, 390, 393.
*Pycraft on the infancy and courtship of animals, 439.
Phototropism, literature on, 394.

*Rat, hearing in, 215.
Rau, P. and N. The biology of mantis, 399, 402, 412.
  homing of wasps, 407, 412.
Révész, G. Vision of night birds, 420, 437.
Reese, A. M. Reactions of newt, 437.
*Reflex, the salivary, 362.
Regen, J. The stridulation of crickets, 407, 412.
Reiff, W. Light reactions of insects, 394, 412.
*Reproduction, the physiology of, 266.
*Rheotaxis, in isopods, 202.
Rheotropism, literature on, 396.
Riley, C. F. C. Responses of toads, 416, 437.
Rojanski, N. A. Materials to the physiology of sleep, 377.
Roubaud. Behavior of wasps, 401.
Runner, G. A. Behavior of beetles, 407, 411.

Sackett, L. W. Behavior of porcupine, 429, 437.
Savitch, A. A. New materials for the study of nutritive reflexes, 377.
Sawyer. Transmission of poliomyelitis, 406, 412.
Schneider, K. C. Thinking horses, 437.
Schwantke, C. Thinking horses, 437.
Seitz, A. Vision in insects, 397, 412.
Sekera, E. Habits of nemertian, 393.
*Severin, H. H. P. and H. C. Behavior of fruit fly, 223, 402.
*Sex, reactions of doves to, 121;
  *behavior in fowls, 266;
  *perception of, 289;
  *behavior in cats, 293;
  *behavior in monkeys, 295.
Sexton, E. W. Habits of *Gammarus*, 390, 393.
*Shelford, V. E. Behavior of fishes, 1;
  *behavior of land animals, 31;
  reactions of fish, 423, 437.
Shephard, J. F. Development of instinct, 426, 438.
*Shepherd, W. T. Sound discrimination by cats, 70.
Sherman, A. R. Habits of hawk, 427, 438.
*Silkworm, perception of sex in, 289.
Skinner, H. Hibernation of house fly, 404, 412.
*Smell, in the dog, 76;
  *in fruit fly, 223;
  literature on, 423.
Smith, L. W. The biology of stone fly, 398, 412;
  biology of *Perla*, 402, 412.
Snail, the behavior of the, 386;
  light response of the, 391;
  mating behavior of the, 391.
Social relations, 384.
*Sparrow, light discrimination in, 79.
Speech, literature on, 407.
*Spider, literature on, 394;
  behavior of, 404.
*Starfish, behavior of, 380;
  locomotion in, 385;
  reactions of, to light, 389;
  vision in, 390.
Statocyst, the function of, 387.
Stauder, H. The biology of *Lysmantria*, 406, 412;
  behavior of caterpillars, 407, 412.
Stevens, H. C. Acquired reactions in crab, 390, 393.
Strand, E. Biology of *Diapalpus*, 406, 412.

Szymanski, J. S. Reactions of snail, 391, 393;
methods of studying instinct, 393;
habit formation in dog and cat, 428, 458.

Taliaferro, W. H. Reactions of amoeba, 388, 392.
*Tashiro, S. Rheotaxis in isopods, 202.
Tchecotareva, O. M. Further contributions to the physiology of conditioned inhibition, 376.
Technique, literature on, 408.
Theocritova, U. P. Time as stimulus of salivary gland, 376.
Thigmotropism, literature on, 396.
Thompson, J. A. Thinking horses, 438.
*Time records for maze, 60.
*Torrey, H. B. The orientation of *Porcellio*, 110;
trials and tropisms, 391, 393.
Townsend, C. H. T. Disease producing organisms, 406, 412.
Trogardh, I. Chemotropism of insects, 394, 412.
Tropisms, 386;
of insects and worms, 391;
and trials, 391, 393.
*Tugman, E. F. Light discrimination in the sparrow, 79.
*Turner, C. H. Literature on behavior of spiders and insects, 394;
behavior of roach, 398, 412;
acrobatic feats of insects, 407, 413;
memory in roach, 408, 412.

Unsicker, migration of moths, 405, 413.
Urban, C. Life history of beetle, 413.

Vassiljev, P. N. Differentiation of thermal stimuli by dog, 376.
Vermes, habits of, 388.
*Vertebrates, vision in, 319;
literature on, 414.
Vesme, C. Thinking horses, 438.
Vestal, A. C. Distribution of grasshoppers, 405, 413.
*Vincent, S. B. Literature on behavior of vertebrates, 414.
Vision, in the sparrow, 79;
*and form perception, 134, 136;
*in insects, 147, 397;
*in the crow, 185;
*pattern discrimination, 319, 340;
*acuity of, 340;
literature on, 414;
*in the starfish, 380;
color responses of crustacea, 386;
color responses of daphnia, 386;
light and color, in octopus, 387;
the color sense of animals, 388;
color response in crabs, 390;
in starfish, 390;
response to color in infusoria, 392;
of fishes, 417.
*Volkelt. Ideas in animals, 442.

Walker, E. M. Sex adaptation, 398, 413;
life zones, 405, 413.
Warrington, Y. Cause of disease, 406, 409.
Wasp, behavior of, 401.
*Watson, J. B. Maze and camera lucida, 56;
development of young monkey, 425, 437;
Watson, J. B. and M. I. Vision in rodents, 438, 414.
Webster. Feeding habits of *Gypona*, 402, 413.
Weiss, H. B. Odor preferences in insects, 394, 413;
behavior of mosquitoes, 395, 413;
thigmotropism of mosquito, 396, 404, 413;
death feigning of weevil, 407, 413.
Wells, B. W. An acrobatic fly, 407, 413.
Wheeler, W. M. Behavior of solitary wasp, 401, 413;
behavior of bees, 403, 406, 413.
Wiegge, C. Thinking horses, 438.
Williams, C. B. Behavior of *Raphidia*, 406, 413.
Winslow, C. E. A. Infant paralysis, 406, 413.
Wodsedalek, J. E. Reactions of dermestidae, 413.

*Yerkes, R. M. A laboratory of Animal Psychology, 176;
heredity in rats, 425, 438.
*Yerkes, R. M. and Kellogg, C. E. Graphic method for maze, 50.
Young, E. The eyes of snails, 391, 393.

Zetek, J. Flight of mosquitoes, 405, 413;
methods for study of insects, 408, 413.
Zimmermann, K. Habits of *Galatheidea*, 391, 393.

JOURNAL OF ANIMAL BEHAVIOR

VOL. 4 JANUARY-FEBRUARY, 1914 NO. 1

RAPID MODIFICATION OF THE BEHAVIOR OF FISHES BY CONTACT WITH MODIFIED WATER

VICTOR E. SHELFORD AND W. C. ALLEE
From the Zoölogical Laboratory of the University of Chicago.

		Page
I.	Introduction	1
II.	Conditions and Methods of Study	3
III.	Experimental Results	6
IV.	Interpretation of Results	22
V.	Bibliography	29

I. INTRODUCTION

At the present time animal behavior is being studied from three or four more or less independent points of view: (1) the point of view of tropisms and reflexes or the study of specificities of behavior, (2) the point of view of positiveness or negativeness to environmental factors—an aspect of ecology or the interpretation of the relation of animals in their normal environments, (3) the point of view of speed or vigor of reactions and of reflexes in relation to the so-called physiological states and their modification—an aspect of physiology, because such states are due to physiological changes such as a change in the rate of metabolism, and (4), the point of view of the modification of behavior by repetition of action or repeated stimulations—an aspect of psychology. Such a separation of view points can be only provisionally made as all are probably resolvable into physiology. Most workers combine two or more of these points of view, so that one type or aspect of behavior acts as an index of another.

The first two view points noted deserve some comment. Specificities of behavior may be defined as those peculiarities of action which characterize species, genera, or even larger groups.

The senior author, for example, is able to distinguish some species of tiger beetles (about one-half inch long) occurring near Chicago, by their peculiarities of flight. Again, ornithologists depend much upon characteristic movements to distinguish species of birds. The details of action in the more stereotyped reflexes of Protozoa and other of the lower invertebrates, such as the backing and turning of Paramecium, are characters of species or of groups of species. These specificities have been much studied by some zoologists, but, like other specific characters, serve chiefly as material for the study of modification, and as characters to be used in cross breeding.

The point of view of ecology is the one of most recent development. It considers all phases of physiology that are related to the life of the animals in their natural environments. The behavior aspects which have been developed center around the following questions: (1) Do animals select their habitats? (2) Is the behavior of the same species different under different conditions? (3) Is there community of behavior among animals of the same or similar habitats? (4) To what factors of the environment do animals respond and what is the degree of the response to the different factors?

A relatively small number of investigations have answered the first three questions in the affirmative, for the particular cases studied. Studies on the effect of particular factors of the environment have been made, but usually with very small animals and under conditions which made accurate measurement and control of the experimental factors difficult. One of the most neglected aspects of physiology and behavior is the reaction of larger animals to the different factors involved in the surrounding medium.

From several points of view the importance of investigations at this point seemed sufficient to more than justify an attempt to determine whether or not fishes react to differences in the dissolved content of the water which they inhabit and whether or not different species differ in their reactions. The data relating to these two questions have been organized and published (Shelford and Allee, '13). Apparent rapid modification of the behavior of the fishes by repeated contact with the treated water was quite characteristic of their reactions and aroused interest sufficient to cause us to go over the results of one hundred experiments from the point of view of modification. This involved re-counting of movements and recalculation of time, etc., which, together with the examination of a large amount of literature has delayed the preparation of this aspect for several months.

II. CONDITIONS AND METHODS OF STUDY

The experiments were conducted under conditions as nearly uniform as possible with respect to all factors except the amount of the various solutes used. (For detailed plans and figure of the apparatus, see Shelford and Allee, '13, pp. 225–229). Two galvanized iron boxes, 120 cm. long by 14 cm. deep by 20.5 c.m wide, with screen partitions 5 cm. from the ends, making the in-

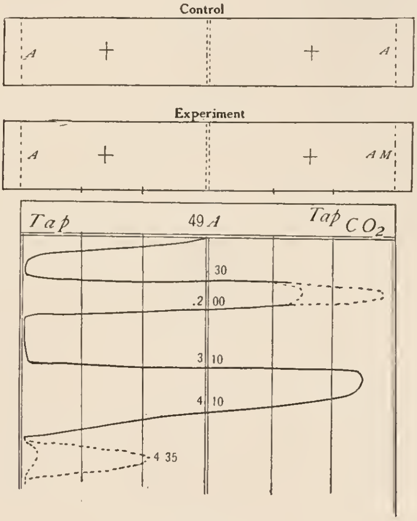


FIGURE I

The upper two quadrangles show the ground plan of the experimental tanks with the positions of the central drain and the lights under which the fishes went when passing to and fro. The positions of the lights are indicated by the crosses and that of the drain by the double broken line near the center. The broken lines near the ends indicate the positions of the screen partitions. The tanks are represented a little less than one-twentieth actual size. The ends *A* receive tap water and AM treated water. Below the tank used for the experiment the method of recording movements is indicated. A portion of the record sheet is shown about twice natural size, and immediately below the reduced tank so that the marks dividing the tanks into sixths are opposite the corresponding dividing lines of the ruled paper. The movements of two mud-minnows during the first five minutes of expt. 49A are indicated with the time of the principal movements, in minutes and seconds after the beginning, shown in figures. The graph is an enlarged copy of the original . The solid line indicates that the two fishes were moving together; the broken line shows the movement of a single fish.

side length 110 cm., were painted dull gray and covered with yellow sand while still adhesive. Water was allowed to flow in at both ends at the same rate (usually 600 cc. per minute) through tees made from iron pipe, the cross bar of which contained a number of small holes. The cross bars of the tees rested on the bottoms of the tanks behind the screens. The drains were transverse tubes with their lower sides made of screen, located near the top and opening outside the boxes. The water flowed in at the ends and drifted toward the center at the top and flowed out through the drain. We found no evidence that fishes react to the slight current thus produced. Since each half of the tanks held about twelve liters, it required twenty minutes to fill them or to replace all the water in one of the halves.

Both tanks were enclosed under a black hood, side by side as shown in the plan (Fig. 1) and were placed about ten centimeters apart. Two four candle power incandescent lights were fixed above the center of the two halves, i.e., above a point midway between the screen partition and the center drain. The light was thirty centimeters above the surface of the water, which was ten centimeters deep. The lights above a given tank illuminated the outer wall of the other tank (see Fig. 1), while the inner wall of the same tank cast a shadow throughout its entire length. The two tanks were identical longitudinally, but the shadow was reversed with respect to points of the compass.

The room was darkened during the experiments, which were observed through openings in the hood above the lights. Fishes do not usually note objects separated from them by a light. The fishes not accustomed to aquaria sometimes showed fright and behaved erratically when first put into the tanks, but all such experiments were thrown out. The main stock of fishes was kept in the laboratory in glass-sided aquaria during the period of experimentation. In this way they became accustomed to an aquarium, to the presence of moving objects, and to variously placed lights.

The purpose of the experiments was to test the reactions of the fishes to a difference in the water in the ends of one of the experimental tanks. Water differing as little as possible from that in which the fishes usually live was introduced at both ends of the other tank in most experiments (control). Treated water from the device already described (Shelford and Allee, '13, p. 214), was introduced at one end of the experimental tank, while water differing as little as possible from that in which the fishes normally live was introduced into the other end. Various kinds of treated water were used as follows: (1) boiled water—oxygen, nitrogen, carbon dioxide, and bicarbonates in part removed; (2) water with varying amounts of carbon dioxide added; (3) boiled water with oxygen added (either against tap or boiled water at the other end); (4) boiled water with either carbon dioxide, acetic acid, or ammonia added. Various combinations of these factors were also tried and nitrogen was added in a few experiments.

When the difference between the solutes at the two ends of the tank was not great, we found by chemical tests that the central portion of the tank was a gradient between the characteristic waters introduced at the two ends. Usually the end thirds were essentially like the inflowing water. When the difference in concentration was great the region of the gradient was proportionally longer and the ends with the inflowing concentrations were accordingly shorter. When the difference in concentration was very great the entire tank was gradient.

During the experiments the two authors worked together. Three fishes were placed in each of two dishes containing enough water to barely cover them and set above the tanks. When all was in readiness and at a time agreed upon the two lots of fishes were emptied into the centers of the tanks. Marks on the sides divided the tanks into sixths. The fishes nearly always swam back and forth apparently exploring the tanks. The movements of the fishes were recorded graphically as shown in figure 1. For this purpose sheets of ruled paper were used. Three vertical double rulings correspond to the center and two ends of the tanks. Two pairs of single rulings divided the space between two primary rulings into three equal parts and the entire distance from right to left into six parts. Distance from right to left was taken to represent the length of the tanks; vertical distance to represent time which was recorded in minutes and seconds at the center. The width of the tanks was ignored. The graphs on the following pages are copies of the originals with the time corrected to scale.

Before or after the experiment, the headings of the sheets were filled in with data regarding the kind, size, and number of fishes, their previous history, the conditions in the tanks, concentrations of the solutes and other significant data. Details of the reflexes of the fishes and notable peculiarities of behavior were recorded in full at the left of the graph. The fishes were observed continuously for from twenty to ninety minutes. In many cases they were caught at the end of such a period of observation in a small hand net and replaced in the small dishes. Observers then changed places and transferred the fishes from one tank to the other. Thus the control fishes of the first experiment were observed in the experimental tank and the experimental fishes were observed in the control tank for a time equal to the first test.

III. EXPERIMENTAL RESULTS

Most of the fishes studied reacted negatively to various concentrations of carbon dioxide; to little oxygen; to boiled water with the removed oxygen restored; and to boiled water with acetic acid or carbon dioxide added (see table 3, p. 20). The behavior of the fishes when giving a negative reaction usually possessed prominent features. They tried the modified water a number of times and then began to turn back in the lower and lower concentrations of the gradient, or to spend shorter and shorter time in the modified water with each visit.

Usually these modifications did not show a uniform gradual decrease in time spent in the modified water or an increasing tendency to turn in lower and lower concentrations of the gradient which extended throughout the experiment. The response was rhythmic rather than cumulative. This may be seen in the charts especially in Expt. 10, chart 1, p. 9, and in controls 78 and 83, chart 2, p. 11. A number of successive trials of the modified water resulted in either a lessening of the time spent in that water or in turnings in the gradient, or both. This led to spending more time in the untreated water. After some time in this water there was again a tendency to enter the treated water with the same results as before. That is, there was a rhythm of reaction, which, while not perfect, was present to a recognizable degree in the majority of cases.

The number of trials of the modified water at the beginning of the experiment was in most instances inversely proportional to the degree of stimulation as indicated by the special activities, except where the concentration was great enough to cause "staggering," or other abnormal reaction. The control fishes on the other hand, went back and forth quite symmetrically.

The results of the experiments on each species were tabulated for the purposes of this paper, as shown for the river chub in table 1, and for the golden shiner in table 2.

TABLE 1

Showing the varying speeds of the modification of the behavior of the river chub (*Hybopsis kentuckiensis* Raf, habitat, small, clear streams) associated with different kinds of modified water. The ratings given in column 3 represent degree of avoidance of the kind of water given first in column 2. The ratings were obtained by averaging per cent of time in the two halves and turnings from the two halves. The rating is 100 when all turnings were from one-half and all the time was spent in the opposite half, and 0 when time and turnings were equally divided between halves. These figures are taken directly from table 20, p. 256 of the preceding paper (of which see pp. 254-57 for further details*). The control rating for the species is ±0 based upon eleven controls.

Number of experiments	Kind of water used, the avoided water standing first	Rating	Difference in amount of oxygen at each end of the gradient in cc. per liter	Difference in amount of carbon dioxide at each end of the gradient in cc. per liter	Total number of individuals	Number of individuals showing modification	Number of invasions of modified water before first turning in gradient	Time in seconds in modified water from beginning to first evidence of modification	Time in seconds in untreated water
2	CO_2 in boiled vs. boiled	97	0	21	6	6	1.0		
2	CO_2 in boiled vs. tap.	94	7	47	6	6	1.8		
1	CO_2 (weak) in tap vs. tap	87	0	5–8	1	1	3.0	110	30
2	CO_2 (strong) in tap vs. tap		0	18	8	6	1.3	169	510
3	Boiled vs. tap	67	7	2	9	9	3.7	95	221
2	Boiled vs. boiled plus oxygen	34	10	0	6	6	4.3	182	91
2	Boiled plus oxygen vs. tap	33	0	2	6	6	3.0	137	85
2	Boiled plus nitrogen plus oxygen vs. boiled plus oxygen. Nitrogen gradient 4 cc.	26	0	0	6	0			
	Totals and averages				48	40 83%	18.1 2.6	693	737

---

* Corrections on p. 255 lines 12 and 13 for "tap water or water nearest like that in which they had been kept" read, more modified water.

CHART I

Showing modification of fish behavior by contact with boiled water, and with boiled with acetic acid added and with boiled water with ammonia added.

Distance between the small vertical lines adjoining the scales at the top corresponds to the length of the tank. The scales represent time in minutes divided into ten-second periods. The horizontal distances in the graphs represent the portion of the length of the tanks traversed by the fishes, the obliqueness of the line as measured by vertical distance and the vertical portions of the graph lines represent respectively the time required to move the distance and the time spent in resting or moving crosswise. The numbers above the generic names at the top represent the number of fishes used. When all or two of the fishes moved together a solid line occurs. The movements of single individuals are shown by broken lines. Double pointed arrows above the tracings indicate the distance occupied by the gradients. When the concentration was high the entire tanks were gradient and the secondary gradient is represented by the lighter double pointed arrows. A corresponding portion of the controls is likewise indicated. The kind of water introduced at the end indicated by the words "tap" and "boiled" the former being the kind of water in which the stocks here discussed were kept. The oxygen content of the water is given in cc. per liter in the vertical wordings where the amount of added solute is indicated also in cc. per liter excepting acetic acid which is given in grams per liter. For statistical purposes (Shelford and Allee '13) the proportion of time in the two halves, the number of turnings in the gradient are used as data.

In experiment 10 the fishes are shown to have entered the boiled water three times during the first two minutes, spending about one-half of their time there. At the end of the two minutes, they began turning back occasionally. This continued until the end of ten minutes when turning became the rule with more or less rhythmic entrance into the treated water. The experiment lasted forty minutes but the remaining ten minutes showed nothing different. When emptied into the control tank the fishes came to rest in one end and remained there for the first twenty minutes, a common reaction when the water is like that from which they were taken. At the end of the twenty minutes the fishes began moving back and forth in a symmetrical manner. Experiment 13 shows the reactions of sun fishes which are representative of the reactions of the fishes studied, to boiled water. The graph of experiment 41 shows a reaction to acetic acid comparable to that given to carbon dioxide. The reaction to ammonia might well be that of a control.

Since three fishes were used it was not always possible to distinguish the different individuals in the experiments and in working over the graphs. In the case of the gregarious species, all three nearly always moved together. With non-gregarious fishes it was nearly always possible to distinguish the different individuals in any one group of invasions of the stimulating water. Individuality was lost only in the periods of rest between invasions. After the graphs were made, the tracing of each fish was followed with red, blue or green ink, the individuals being followed so far as possible, but where individuals were lost during a period of rest each tracing was continued without conscious reference to what the individuals had done previously. This was due to the fact that the tracings were made as a basis for calculating time spent in the two ends and before any discussion of modification was in mind. The individuals are then, where not clearly distinguished, treated in a chance fashion, and should show the same average result as the actual movement of the individuals. The comparisons of species and factors are valid because such errors as occur are present in all the experiments and we believe that any errors arising from failures to distinguish individuals are of minor significance.

CHART I

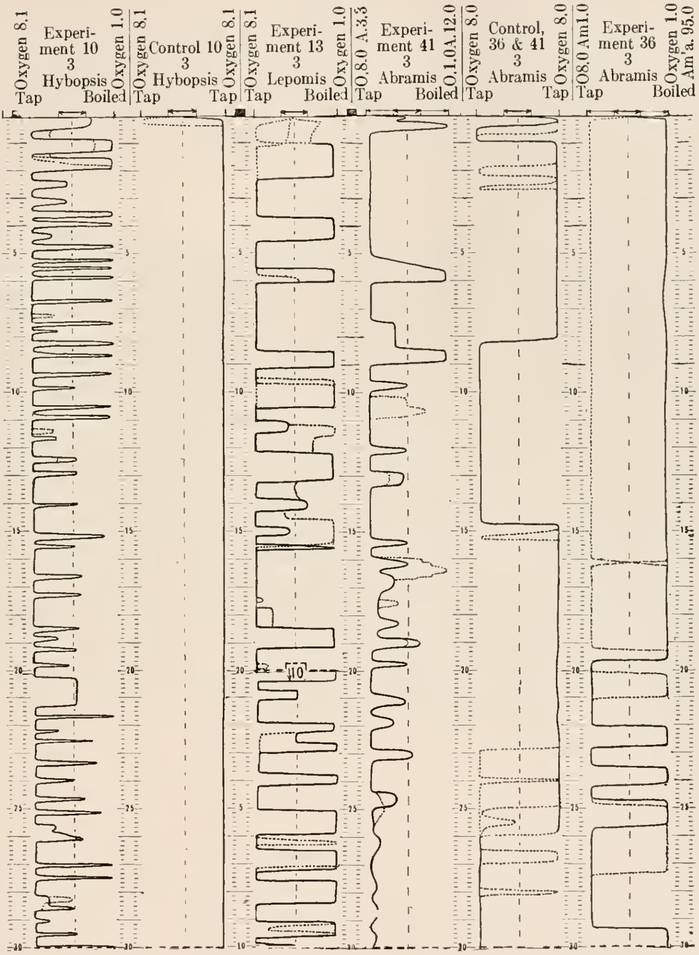

Oxygen 8.1
Experiment 10
3
Hybopsis
Oxygen 1.0
Tap
Boiled
Oxygen 8.1
Control 10
3
Hybopsis
Oxygen 8.1
Tap
Tap
Oxygen 8.1
Experiment 13
3
Lepomis
Oxygen 1.0
Tap
Boiled
O.8.0 A.3.3
Experiment 41
3
Abramis
O.1.0A.12.0
Tap
Boiled
Oxygen 8.0
Control, 36 & 41
3
Abramis
Oxygen 8.0
Tap
Tap
O8.0 Am1.0
Experiment 36
3
Abramis
Oxygen 1.0
Am'a. 95.0
Tap
Boiled
5
10
15
20
25
30
10

Chart II

Showing modification by contact with boiled water, with boiled water plus oxygen to balance that of the tap water, and with tap water plus carbon dioxide. For further explanation see Chart I. In experiment 78, *Hybopsis* did not react to the effect of boiling with the oxygen factor eliminated but did react to the boiled water. At the end of about two minutes after all the fishes had tried the boiled water several times, the turnings in the gradient began, and the same type of modification was again shown (see Chart I). *Ambloplites* reacted to both the boiled water and the boiled water with oxygen added. Detailed study of these fishes from the side in the boiled water while in glass boxes showed that the respiratory movement was increased but that other activity was depressed, this species being an exception in the matter of depression. However, in both parts of experiment 83, after the fishes had tried the water in both ends several times they began to turn back and make shorter stays in the modified water.

Experiment 53 shows the reaction where sufficiently high concentration of carbon dioxide was used to produce death in less than an hour. Under these conditions the fishes did not turn back until two had tried the high concentration. The third fish turned with the other two without entering the high concentration, a thing which takes place normally in a gregarious species and thus can hardly constitute a real exception. The graph is typical of the whole series of experiments until the end of eight minutes when the movements become erratic due to the effect of the carbon dioxide upon the fishes. In a later experiment with only a slightly larger amount of carbon dioxide the fishes ceased to react properly after a short time and turned upon their backs.

CHART II

Arrows indicate that the fishes were driven

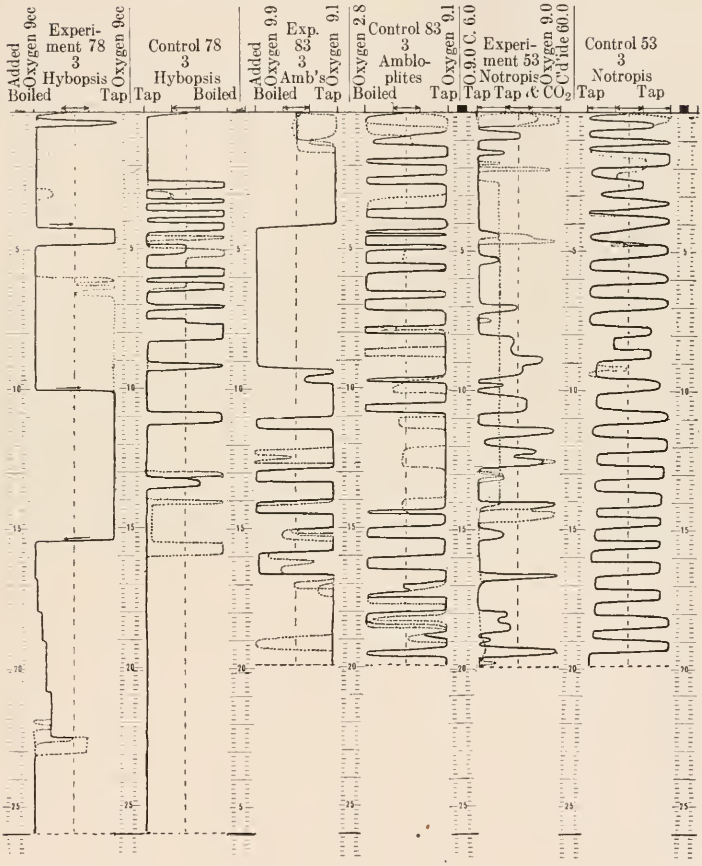


CHART III

Showing modification by contact with boiled water with 50 cc. per liter of carbon dioxide added. For further explanation see Chart I.

In these experiments the fishes tried the gradient of the entire tank a number of times and then either remained in one end except when driven as indicated by arrows, or turned back often before the center was reached. For example *Hybopsis* (experiment 56) entered the modified water once or twice and then came to rest in the low concentration, invading the high only when driven with the exception of a single excursion which followed a disturbance. The graph of *Ameiurus* shows one of the very few cases in which the fishes turned back before the strongest stimulus had been encountered. Still the graph brings out the same general fact of modification. The gradient in experiment 76 was established with some difficulty as the nitrogen was only 93% of the gas available the rest being oxygen. Boiled water had to be used at both ends and sufficient oxygen added at one end to balance the oxygen added with the nitrogen at the other. Even here, with the factors involved somewhat in doubt, the same modification is suggested.

CHART III

Arrows indicate that the fishes were driven

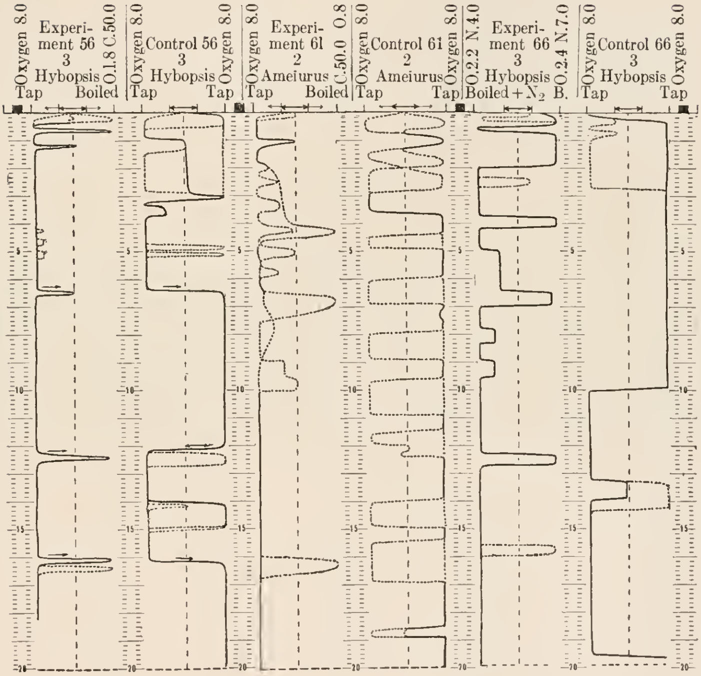


CHART IV

Showing the establishment of apparent preferences by groups of individuals of Abramis.

In experiment 1A an apparent preference already existed for the right hand end. An apparent preference for the left hand end was established and broken again by introducing boiled water as indicated. In experiment 84 the graphs of experiment and control are very similar during the first ten minutes. The apparent preference for the left hand end of the control tank was modified and apparently broken by repeated drivings indicated by arrows, and by confining the fishes in the avoided end during the nineteenth minute. The control fishes of experiment 58 established an apparent preference for one end after ten minutes and for reasons unknown. For further explanation see Chart I.

CHART IV

Arrows indicate that the fishes were driven

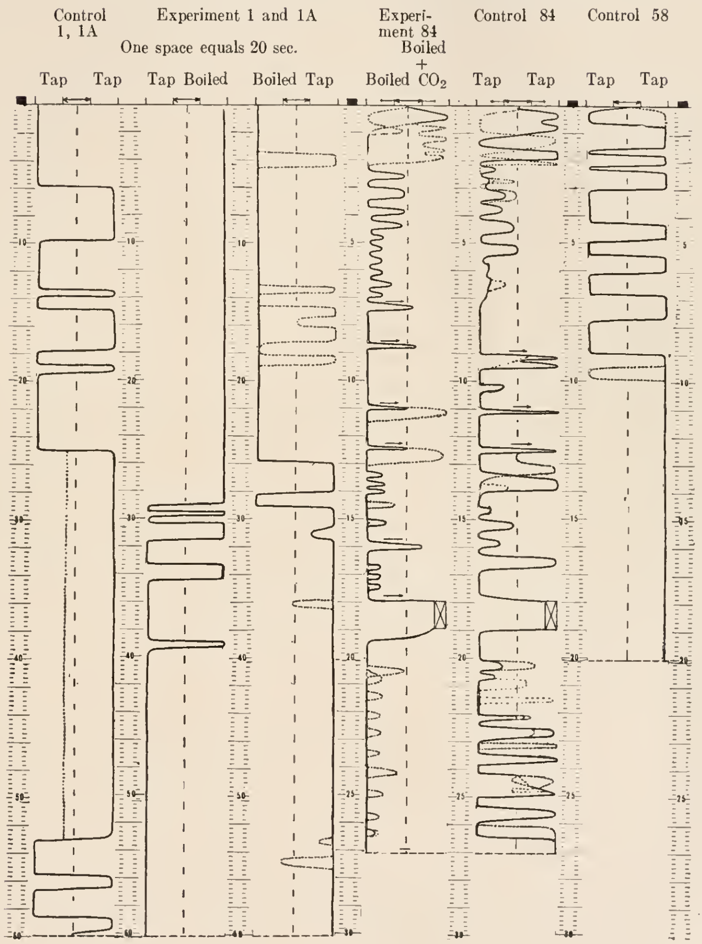


TABLE 2

Showing the varying speeds of modification of the behavior of the golden shiner (*Abramis crysoleucas* Mit. Habitat, stagnant ponds.). The rating of the controls ±11 is based on 15 controls. For further details see table 1.

Factor or factors, avoided water first	Rating	Difference in amount of oxygen at each end of gradient in cc. per liter	Difference in amount of carbon dioxide at each end of gradient in cc. per liter	Total number of individuals tested	Number of individuals showing modification	Number of invasions of modified water before first turning	Time in seconds in avoided water from beginning to first sign of modification	Time in seconds in untreated water from beginning to first evidence of modification
CO_2 in boiled vs. boiled. .	85	0	21	6	6	1.8	63	71
CO_2 in boiled vs. tap	91	7	47	6	6	3.6	52	268
CO_2 (weak) in tap vs. tap	60	0	5	3	3	2.0	43	62
CO_2 (strong) in tap vs. tap		0	65	6	6	3.5	66	96
Acetic 12 grms. per L. in boiled vs. 3.3 grms. per L. in tap.	85	7	2	2	2	3.0	215	485
Boiled vs. tap.	75	7	2	9	4	4.0	202	262
Boiled vs. boi.ed plus O_2.	75	10	0	3	?			
Boiled plus O_2 vs. tap. . . .	39	0	2	3	?			
Boiled plus NH3 85 cc. per L. vs. tap 1 cc. per L.	8	7	2	2				
Totals and averages. . .				40	27 67%	17.9 2.98	641	1244

The behavior of Hybopsis is further illustrated in chart 1, Expt. 10, the data from which are included in the table. It will be noted that in the reaction recorded in the chart the three fishes first turned back after two invasions of the boiled water and that turnings occurred more often than entrances after fifteen trials of the boiled water. It will also be noted that the entrances of the boiled water toward the end of the experiment occurred only after some time had been spent in the untreated water. In this case there was less activity in the control as the fishes remained in one end for thirty minutes and then (see below graph of Expt. 13) began to go back and forth more slowly than in the experiment. Two turnings at the center are shown by the control fishes and these are opposite in direction. This shows that the fishes sometimes turn in the absence of solutes.

A comparable result with boiled tap water is recorded in chart 2, Expt. 78 (control). Here the turnings are less prominent and shortened stays in the boiled water were followed by resting in the tap water. In the part of Expt. 78, where the amount of oxygen was the same at each end of the gradient there is no evidence of modification, but simple disturbance is indicated. This shows that the fish sense the effects of boiling even when there is a normal amount of oxygen in the boiled water. In chart 3, Expt. 56, very rapid modification is indicated, and after the first few trials of the modified water the fishes stayed in the tap water end, except when driven out (indicated by arrows). In the same chart, Expt. 66 shows an apparent modification due to the introduction of an atmosphere of nitrogen and oxygen. This atmosphere had an oily odor which may have affected the results obtained.

Expt. 13 of chart 1 and Expt. 83 of chart 2 show the type of mild negative reaction with indications of slight modification given by the sunfishes and basses tried. The graph of Expt. 53, chart 2 shows the symmetrical type of control most common with Notropis and a case of somewhat erratic action in very strong carbon dioxide after it has time to seriously affect the fishes.

The graphs of Expts. 41 and 36 of chart 1 show the reaction of Abramis to acetic acid and ammonia in boiled water. On encountering the acetic acid the fishes often gave a definite reflex—the " backing-starting " reaction to be described on page 24. The reaction to acetic acid in boiled water compares very favorably with that to carbon dioxide in boiled water. Such a reaction is shown in Expt. 84, chart 4. The ammonia experiment shows the failure of the animals to react negatively to this factor, although the backing-starting reaction occurred more often than in the acid. The fishes died in the ammonia.

The case of Abramis demands special attention as this is the only species studied in which the groups of individuals developed apparent preference for unknown reasons. In this species this peculiar trait seems to be well developed. It avoids mild stimuli by rhythmically shorter stays in the modified water and stronger stimuli by turning back in the gradient. The general behavior when turnings are being given is shown in table 2.

In our earliest experiment with Abramis we obtained no results because the fishes remained in the tap water and so failed to encounter the treated water. It was noted also that when these fishes were left in the tanks they tended to stay in one end or the other. This led to the following experiment: Three individuals were placed in each tank with the same kind of water flowing into both ends of each. After both groups had developed an apparent preference for one end, the fishes selected for the control of the experiment to follow were disturbed until they tended to go back and forth. At the same time a shadow was thrown over the end of the tank selected for the experiment opposite to that in which the fishes were staying. The experimental fishes were driven into this shadow several times and soon developed an apparent preference for the shaded end of the tank. The fishes to be used for the experiment were left in the shadow for about two hours. The fishes to be used for the control were driven from end to end several times during this period. The apparatus was then arranged for the introduction of treated water which necessitated the removal of the shadow. Even after the shadow was removed and the apparatus was disturbed, the fishes persisted in their apparent preference for the end which had been shaded (Edinger, '01; Holmes, '11). Boiled water was introduced in the end in which the fishes were staying. The results of this part of the experiment are shown in Expt. 1-A, chart 4. In the control, the time was divided between the two halves in the ratio of 41 to 59 for the hour of the observation. During the same period the experimental fishes stayed in the boiled water end during the first 29 minutes, when they began going back and forth. They clearly stayed a little longer in the tap water with each excursion. After making five trials of the tap water in a trifle more than ten minutes the fishes came to rest in the tap water end and remained there until the completion of the hour's observation. The boiled water introducer was then placed in the newly "preferred" end and similar results were obtained modified only by the additional activity of a juvenile individual.

In Expt. 84, chart 4, the same species showed a comparable reaction. The control fishes avoided the end corresponding to the carbon dioxide end of the experiment as clearly as did those in the experimental tank. When they were confined in the avoided end the apparent preference for the other end was broken in the control, but only strengthened in the experiment. In the control of Expt. 58, Abramis established an apparent preference for the end avoided in Expt. 84. Since Abramis does not rest on the bottom, this reaction might be thought to be parallel to the resting of other fishes (chart 1, Expt. 10), were it not for the fact they that choose one end after visiting both many times, while others usually come to rest after the dash which follows their being poured into the tank. The behavior of Abramis in these controls was similar in many respects to the avoidance of carbon dioxide and acid given by this fish and others in the experiments. That is Abramis sometimes reacted positively to one end when tap water was running into the two ends from the same pipe at the same rate. The fishes do not appear to have any special tendency to rest near objects. They may sense the current at the end, but we have no evidence that such is the case.

These apparent preferences of Abramis demand further experimentation for their analysis. From the work so far they apparently do not belong in the same category as the rest of the reactions described here and may be due entirely to associative memory. Although if this be true the associated elements are at present unknown.

A general summary of the data on modification is contained in tables 3 and 4. In table 4, the various species are arranged roughly in the order of their sensitiveness. Later work by Mr. M. M. Wells has shown that the data in columns three and four are not accurate, because the time to loss of correlation or until "staggering" occurs is rather indefinite and difficult to determine. He uses the time until death. However, the data represent relative sensitiveness in a general way. The time required to accelerate the respiratory movements in low oxygen is likewise difficult to determine, but the data presented are more reliable than that in the two preceding columns. The remaining data are concerned with the number of trials before evidence of modification was given by turning. This is a definite criterion and does not seem open to serious criticism. Reading 6, 7, 8 and 9 from top to bottom, we note that generally speaking the less sensitive fish show the greatest number of trials of the modified water before giving evidence of modification. In columns 10 and 11, we note that the percentage of individuals showing modification is greatest in the more sensitive species and that when all are reduced to terms of 100 per cent. of modification the most sensitive species show the smallest number of trials before turning. The time in the two kinds of water is variable, but usually greatest in the unavoided water.

Reading the lines from left to right we note that the sensitiveness of the fishes is different for different stimuli.

TABLE 3

A list of the species used; the size of the individuals; physiological relations to the factors used; number of turnings and time spent in each half before modification was apparent.

1	2	3	4	5	6	7	8	9	10	11	12	13
SPECIES (Individuals used, chiefly juveniles)	Length of fish in centimeters	Seconds to loss of correlation in water with 1 cc. O_2 and 163 cc. CO_2	Minutes to loss of correlation in water with less than 1 cc. O_2	Seconds to modify respiration in water with 1 cc. of oxygen	Boiled CO_2 47 cc. vs. tap. No. trials before modification	Tap, CO_2 65 cc. vs. tap. No. trials before modification	Boiled vs. tap. No. trials before modification	Average number of trials before modification	Per cent showing modification	No. of entrances before modification reduced to basis of 100%.	Seconds in avoided water before modification. (Ave. of all expts.)	Seconds in avoided water before modification. (Ave. of all expts.)
Micropterus dolomieu Lac.	8–9		20	40			6	6	100	6.0	257	215
Notropis cornutus Mit.	5–9	60	376	45	1.0	0.8		1	100	1.0	97	108
Hybopsis kentuckiensis Raf.	7–10	50	355	50	1.8	1.8	3.7	2.3	100	2.3	251	108
Ambloplites rupestris Raf.	5–9	180	340	55	1.0	1.5	5.4	2.6	58	4.5	200	119
Catostomus commersonii Lac.	8–11	300		60	1.3	2.3		1.8	60	3.0	95	110
Abramis crysoleucas Mit.	6–15		400	60	3.6	3.5	4.0	3.5	67	5.8	268	87
Etheostoma zonale Stor.	3–5			150					0		20	20
Lepomis cyanellus Raf.	4–6	150		300	2.3	3.5	2.5	2.8	60	4.6	146	165
Ameiurus melas Raf. Low O_2	13–15			350							5	
Ameiurus melas Raf. High O_2	13–15		1800	270		2.3		2.3	40	5.7	53	30
Umbra limi Kirt.	10–13						19.6				106	81
Totals					11.0	15.8	41.2	22.3	585	32.3		
Averages					1.8	2.2	6.8	2.8	65	4.0	159	104

In general the fishes were found by other criteria to be most sensitive to high carbon dioxide in boiled water, to high carbon dioxide in tap water, and to boiled water (low oxygen). It will be noted that the fishes showed modification with fewest trials of the type of water to which they are generally most sensitive. There are several exceptions to this, but the averages of all the species show this very clearly.

TABLE 4

Showing the speed of modification due to different conditions

	Experimental factors. Avoided conditions precede "vs"									
	CO_2 in boiled vs. boiled	Acetic acid in boiled vs. tap	CO_2 in boiled vs. tap	CO_2 in tap vs. tap		Boiled vs. tap		Boiled vs. boiled plus O_2	Boiled plus O_2 vs. tap	Boiled plus NH_3 (strong) vs. tap plus NH_3 (weak)
				Strong	Weak	High O_2 Stock	Low O_2 Stock			
No. of species tried . .	2	1?	8	8	5	9	1?	6	6	2
No. of individual trials. Grand total, 230	12	4	38	45	9	35	23	33	27	4
Per cent of individual trials showing modification by turning	100	100	71	97	100	60	61	51	55	0
Ave. No. invasions of stimulating water before turning (modification)	1.4	2.7	1.8	2.1	2.1	4.4	3.8	4.7	5.5	
Ave. secs. spent in modified water before turning (modification)	30	147	30	119	62	205	86	99	174	
Ave. secs. spent in untreated water before turning (modification)	138	226	167	219	66	438	100	99	346	

Table 4 shows for the types of modified water shown in detail for all the species and individuals (230 in all). An examination of the table shows the same general relations as have been brought out for the particular species. The average time spent in the two kinds of water is least in the water producing the modification in all cases save one and in that the time in the untreated equaled that spent in the modified water.

IV. INTERPRETATION OF RESULTS

The phenomenon discussed and illustrated by the graphs on the preceding pages is clearly one of rapid modification. The behavior of the fishes was different after from one to four entrances into the end where the stimulation was greatest. This modification is indicated by the two types of behavior suggested above, viz.: (1) Turning in weaker and weaker parts of the gradient; (2) By making shorter and shorter stays in the modified water. This last type of behavior is not considered in the tables, since it cannot be readily tabulated because of its rhythmic nature.

In general, fishes swim about either continuously or periodically when in normal water and under uniform light conditions. This tendency under the unnatural conditions of the experimental tanks is strong and though some species may rest for considerable periods in the control tank, they periodically move from end to end. The fishes move crosswise of the tanks but this was not considered, since it appeared to be a minor matter because of the narrowness of the tanks. Furthermore, it bore no relation to the experimental conditions other than to prolong the time spent in a particular part of the tank.

The modification, which will be chiefly discussed, consisted of breaking the tendency to swim to the end of the tank and of substituting turnings at points of weaker and weaker concentrations of the experimental factor or factors. The tendency to pass to the end of the tank as opposed to turning nearer the center may not be markedly strong, for all the fish occasionally turned and swam back or swam about in circles without crossing the center (see chart 1, column 3, last ten minutes of the control of Expt. 10). Still, on account of the small size of the tanks, this tendency is apparently almost as strong as the tendency of fish to swim anywhere when not especially stimulated. No doubt it is about as strong as the tendency of Möbius' pike

(Holmes, '11) to strike its nose against the glass partition, and from the standpoint of the fishes in relation to nature, modification by contact with stimulating water is of a more significant type.

Any explanation of the modification demands first a clear statement of the problem. With figure 1 before us, this statement together with a discussion of various possible explanations will be made. One explanation that may be advanced is that the fishes were depressed by the modified water and thus tended to stop swimming forward on entering it and so finally came to rest in the normal water. This is very clearly not the case, although it is suggested by some of the graphs because the cross movements of the fish are not indicated. With one exception, the modified water was stimulating. The exception was a temporary depression of activity of the rock bass due to lack of oxygen. In a few experiments, the rock bass entered the boiled water and, being depressed, stayed there a half hour or more. Finally, however, they began to move back and forth and selected the tap water end.

Another explanation is that the fishes are stimulated by the modified water and thus move out of it more quickly and spend more time in the untreated water. This is clearly what happened in many cases. The fishes rushed forward more rapidly when they encountered the stimulating conditions, and upon reaching the end, turned and moved out quickly. Still, this does not explain the turning in the gradient which took place more often than the simple acceleration. Neither does it explain what was also sometimes true, namely, that fishes did not show the acceleration until they had encountered the treated water a number of times.

A third explanation that may be advanced is this: When the fishes had been exposed to the low oxygen water or to water containing much carbon dioxide for a long enough time to affect the oxygen or carbon dioxide content of much or all of the blood and thus affect the nervous system as a whole, the fishes began to turn back. The change in gas content caused a change in the physiological state of the fishes, so that they were more sensitive to the surrounding medium. In connection with this explanation, and the preceding one as well, certain facts brought out in the experiments should be noted. When dropped into water containing 150 cc. or more of carbon dioxide and only 1cc. of oxygen per liter, very striking evidences of stimulation appear almost instantly. In 47 cc. of carbon dioxide per liter in boiled water nearly all the fishes showed evidence of stimulation at once. They would start gulping before reaching the end of the tank on the first entrance of the solute. In only a few of the cases was this delayed as long as 50 seconds. In from 20 to 60 cc. of carbon dioxide per liter in tap water the fishes showed similar stimulation in from two to ten seconds after entering the high concentration. In boiled water some fishes showed increased activity, gulping within ten seconds, but such manifestations were frequently delayed for nearly a minute and were quite variable in intensity. In acetic acid the evidences of stimulation were similar to those in carbon dioxide and in ammonia some of them were noticeable.

The fishes undoubtedly sense the solutes upon entering them. For this, they give evidence by the following activities: A definite reflex was often given by Abramis, Notropis, Hypopsis and Lepomis the first time they entered the modified water. The fish suddenly stopped, backed quickly a few millimeters and then started ahead again, often repeating the reflex before going farther forward. In the earlier paper, we called this the backing-starting reaction. This may be due to stimulation of the nostrils. Sheldon ('09, p. 278) states that stimulation of the nostrils of the dog fish resulted in a quick jerk of the head. There was acceleration or increased vigor of movement of fins, tail or body which began at once or after a very short time. Sheldon found that the application of solutions to these parts caused them to be moved. The opercles were lifted, the lower jaw protruded, or the mouth moved in a manner characterized as coughing, gulping or yawning. Sheldon found that stimulation of the mouth or spiracle gave rise to violent gulps. In our experiments these reactions occurred singly or in combination. The time necessary to produce them was variable, but depended upon the strength of the stimulus, which confirms further observations by Sheldon ('09).

As further evidence of the quick sensing of the stimuli, Hybopsis turned back the first time the gradient was tried in nine cases, Notropis in three cases, Ameiurus in four cases, Umbra in one case, and Abramis in one case. With a single exception carbon dioxide was the factor thus avoided. This is good evidence that fish ascertain the condition of the water by peripheral sense organs or otherwise. The modifications appearing after a number of trials must be due to increased sensitiveness to the modified water or to associative memory or to both.

The physiological explanation which may be made for the increased sensitiveness with increased exposure to water high in carbon dioxide is simple, and is based largely upon the relations of organisms to carbon dioxide. The arterial blood of dogs and horses (Hill, '06) has been shown to contain 330–550 cc. per liter of carbon dioxide, free and combined. The free carbon dioxide is about 20 cc. per liter, so in most of the concentrations used more carbon dioxide would be taken up (Hill, '06, p. 533) and its removal from the blood and tissues was undoubtedly hindered in all cases. Since carbon dioxide is constantly produced inside the fish's body the effect of increased concentration on the outside would become greater with repeated trials of the carbon dioxide water. Waller ('96) has shown that carbon dioxide in small amounts increases the irritability of nerves. Hill ('09) states that similar results have been obtained with micro organisms.* A stimulating concentration of carbon dioxide is generally recognized among physiologists. Because of the increase in internal carbon dioxide brought about by entrance into the carbon dioxide water, the fishes tended to become more sensitive with repeated entrances and hence to turn back in weaker concentrations. After spending some time in the weaker carbon dioxide of the tap water end of the gradient tank, they partially recover and tend to resume their usual movements. This brings them again into the modified water and the process is repeated, hence we have a rhythmic invasion of the carbon dioxide water as shown in chart 1, Expt. 10.

As was noted in table 3, the respiratory center is stimulated and the respiration movements increased in carbon dioxide and in low oxygen. This requires more time than the reflexes which follow the sensory impressions (Westerlund, '06). In carbon dioxide the increased respiratory movements occur within a few seconds after the reflex movements. The same is true in low oxygen, where respiratory changes have been definitely timed (table 3). Our evidence indicates that peripheral stimulation is not of supreme importance in the regulation of breathing, because the fishes reacted definitely to a change in the water before the breathing was affected.

---

*The sensitiveness of fishes to carbon dioxide probably increases with starvation. A stock of fishes kept during the winter of 1911–12 without food showed markedly low resistance in that they lost their equilibrium in from 30 to 50 cc. of carbon dioxide per liter.

Bethe ('03) proposed the hypothesis that the breathing rate of fishes is regulated directly by stimulation from the periphery, particularly by stimulation of the mucous membrane of the mouth and gills. This hypothesis has been widely tested (Baglioni, '10 and citations), but the more recent experimentation (Reuss, '10) seems to show that the breathing of fishes is regulated indirectly as in the higher vertebrates, although the suggestion of Kuiper ('07) that both the automatic center and reflex stimulation are concerned has much evidence in its favor. The important thing in the work of the followers of Bethe from the standpoint of this paper is the establishment of quickly working sense perception in the mucous membranes of the gills and mouth.

The negative reaction and modification of reaction of fishes to acid may be explained in a manner similar to that presented for carbon dioxide. Winterstein ('11), Signorelli ('10) and Quagliarello ('11) and others report that it is the acidity of the blood that affects the respiratory center and similar results are nearly always obtained with carbon dioxide and other acids in reversing reaction to light, etc. (Mast, '11 and citations). Accordingly the increased sensibility in acetic acid and in carbon dioxide probably have a common explanation.

It is well known that an insufficient supply of oxygen leads to the formation of lactic acid rather than carbon dioxide as the end product of respiration. Fletcher ('98), Fedman and Hill ('11) and Araki ('91) report that lactic acid production bears some inverse relation to oxygen supply. Signorelli ('10) found that lactic acid directly affects the respiration center.

When the fishes remain long enough in the low oxygen to affect the amount of oxygen in the blood and tissues, the presence of lactic acid probably results and the plasma tends toward acidity just as when acids are used directly. We thus infer that increased sensibility and the resulting modifications are due to acidity just as in the other two cases.

Ammonia is present in the blood of mammals and appears to bear some relation to the carbon dioxide (Hopkins and Dennis, '11). The failure of the fishes to react to ammonia accords with the known effects of the drug. According to Cushny, when ammonia or its common salts are absorbed by the blood, it is not rendered more alkaline but the ammonia is rapidly changed to urea and excreted. The effects of the kation on the common frog is to paralyze the terminations of the motor nerves. While the effect upon the sensory ending appears not to have been investigated, paralysis appears to have occurred in the fishes studied. Frogs and mammals usually die from ammonia poisoning in tetanic convulsions as did the fishes used in the experiments.

It may be noted that the stimuli which give rise to the modifications most quickly are those commonly encountered by fishes in nature. Ammonia, which is rarely encountered in any considerable quantity, did not give rise to a modification and not even to an avoiding reaction. Again the darters are swift stream fishes, depending upon mechanical conditions to maintain themselves in a suitable environment. They rarely encounter carbon dioxide or low oxygen and failed to react to them at all quickly, although they were affected by both. Advantageous reactions appear to be confined to stimuli commonly encountered in the normal life of the animal. By this we mean merely to imply that whatever the processes of origin and survival may have been in detail (Mathews, '13), there is correlation between the conditions of existence and types of irritability (Henderson, '13).

It thus seems probable that associative memory does not necessarily play any rôle in the process of modification described. Since the experiments were conducted with a view to eliminate any possible effects of learning, only incidental evidence was acquired. The treatment of the stock of fishes was as follows: There were a number of individuals of each species in the aquaria, and individuals were drawn at random for each experiment. A given series of experiments were run and the fishes were returned to the aquaria and not used for experiments until several days had elapsed. In nearly all cases the same fishes were used only by chance. When it was necessary to repeat an experiment on the same day, different fishes were used except in one or two cases not included here.

Apparently, in experiments thus conducted, evidence of retention can be of two kinds. These are indicated by the following questions: After entering the modified water a number of times and turning back, did the fishes often turn back before reaching the gradient ? When transferred to the control after exposure to the gradient did they turn back, or show a preference for either end of the control ?

The first type of behavior could be shown only where the gradient was confined to the central third of the tanks. Since some species turn in any part of the tanks it is necessary to select a particular species which does not show this trait. Hybopsis was our best example of this for normally they went back and forth symmetrically in the controls. The graphs indicate that in the boiled water experiments this species turned back often before the gradient was reached, which raises the question as to whether they associate the center drain or difference in lighting with stimulating water ahead.

Fishes are able to form associations (Möbius fide Holmes, '11 and many others). There appear to be two ways in which associations formed in the experimental tanks could be carried over to the control tanks. One is through the kinaesthetic sense, the other through differences in illumination of the sides of the body when approaching the drain from the different directions. The data which we have upon this question comes from comparing the responses in the first and second halves of the double experiments described on page 6.

It is obvious that if the fishes were able to associate the differences in illumination upon the sides of the body when approaching the drain, with increasing stimulation further on in the gradient and were able to retain this after being dipped out of the water with a net and placed for a short time in very different surroundings, they should show an apparent preference for the end of the control tank opposite that in which they spent most time in the experiment. (cf. Fig. 1). An examination of the records of twenty-eight controls indicates that the fishes usually showed some difference in their relations to the two ends of the control tanks, but in these exchanged controls less than half of the fishes show an apparent preference for the end that should have been favored if the light was depended upon. This is as it might be if the kinaesthetic sense were depended upon for the reaction, but the number of experiments is too small to make the slight difference more than a chance one. The comparison of the reactions in the experiment with those of the succeeding controls only serve to emphasize former findings that the solute is the chief guide in the reactions of the fishes.

Special investigation would be necessary to determine whether or not associative memory plays any rôle, but if so, it might be due to an association of increasing stimulation with stronger stimulation further on in the gradient. There is a more or less distinct rhythm of the reactions in the gradients and the view of associative memory applied to this phase of the reaction would call for a make and break of associations so rapid as to cast doubt upon this being the entire explanation. And, since the increased sensibility due to repeated stimulation is explainable otherwise, the assumption of learning, as applied to this aspect of behavior, is as unnecessary as it is questionable. Still, while we have thus separated the type of modification here described from associative memory by the use of the usual criteria, we do not mean to imply that the processes involved are necessarily fundamentally different.

IV. ACKNOWLEDGMENTS AND BIBLIOGRAPHY

The authors are indebted to Dr. Harvey A. Carr, Dr. Tashiro and to Mr. M. M. Wells for suggestions during the preparation of the manuscript.

BIBLIOGRAPHY

For further citations, see Shelford and Allee, 1913.

ARAKI, T. Ueber die Bildung von Milchsäure und Glycose im Organismus bei 1891. Sauerstoffsmangel. *Zeit. f. Physiol. Chem.*, XV, p. 335.
BAGLIONI, S. Zur Vergleichenden Physiologie der Atembewegungen der Wirbel-1910. tiere. *Ergeb. der Physiol.*, Vol. 9, pp. 90–137; 1911, Vol. 11, pp. 526–597.
BETHE, A. Algemeine Anatomie und Physiologie des Nervensystems. Leipzig. 1903.
CUSHNY, A. R. Pharmacology and Therapeutics, 10th edition, pp. 498-501 Phila-1910. delphia.
EDINGER, L. Haben die Fische ein Gedächtniss? *Allg. Zeitung.* (Trans in Smith-1899. sonian Rep., 1899, p. 375.)
FEDMAN, I. and HILL, L. The influence of oxygen inhalation on the lactic acid 1911. produced during hard work. *Jour. Phys.*, Vol. 42, pp. 439–443.
FLETCHER, W. M. The survival respiration of muscle. *Jour. Physiol.*, Vol. 23, 1898. pp. 10–99.
HOPKINS, R. and DENNIS, N. Interrelation of the Ammonia and Carbon dioxide 1911. Content of the Blood. *Jour. Bio. Chem.*, Vol. 10, pp. 407–415.
HOLMES, S. J. Evolution of Animal Intelligence. New York. 1911.

HENDERSON, L. J. The Fitness of the Environment. New York.

HILL, L., (ed.) AND OTHERS. Recent Advances in Physiology and Biochemistry.
1906. London.
1909. Further Advances in Physiology. London.

KUIPER, T. Untersuchungen uber die Atmund der Teleostier. *Pflügers Arch.*, 1907. Vol. 117, pp. 1–107.

MAST, S. O. Light and the Behavior of Organisms. New York. 1911.

MATHEWS, A. P. Adaptation from the Point of View of the Physiologist. *Amer.* 1913. *Nat.*, Vol. 47, pp. 90–104.

QUAGLIARIELLO, G. Influenza delle injezione endovenose di acido cloridrico sulla 1911. respirazione. *Arch. di Fisiol.*, Vol. 9, pp. 477–484 (fide Baglioni '11.)

REUSS, H. Die Wirkung der Kohlensaure auf Atmung der niederen Wirbeltiere, 1910. in besonderen der Fische. *Zeit f. Biol.*, Vol. 53, pp. 555–587.

SHELDON, R. E. The Reactions of Dogfishes to Chemical Stimuli. *Jour. Comp.* 1909. *Neurol.*, Vol. 19, pp. 273–331.

SHELFORD, V. E. and ALLEE, W. C. The Reactions of Fishes to Gradients of dis- 1913. solved atmospheric Gases. *Jour. Exp. Zool.*, Vol. 14, pp. 208–266.

SIGNORELLI, E. Influence de l'acide lactique sur la fonction du centre respiratoire. 1911. *Arch. ital. d. Biol.*, Vol. 55, pp. 119–128 (fide Baglioni '11).

WESTERLUND, A. Studien uber die Atembewegungen der Karausche mit beson- 1906. derer Ruchsicht auf den verscheidenen Gasgehalt der Atemwasser. *Skandinav. Arch. f. Physiol.*, 1906, pp. 263–280 (fide Baglioni '10).

WALLER, A. D. On the Influence of Reagents on the Electrical Excitability of 1896. Isolated Nerve. *Brain*, Vol. 19, pp. 44–67.

WELLS, M. M. The Resistance of Fishes to different Concentrations and Combi- 1913. nations of Oxygen and Carbon dioxide. *Biol. Bull.*, XXV pp. 323-347.

WINTERSTEIN, H. Die Regulierung der Atmung durch das Blut. *Pflügers Arch.*, 1911. Vol. 138, pp. 167–184.

MODIFICATION OF THE BEHAVIOR OF LAND ANIMALS BY CONTACT WITH AIR OF HIGH EVAPORATING POWER

VICTOR E. SHELFORD

Hull Zoological Laboratory, University of Chicago

I. INTRODUCTION

The rapid modification noted in the case of fishes, by the author and Dr. W. C. Allee is likewise shown by various land Amphibians and Arthropods, used in experiments designed to test the sensibility of different terrestrial animals to variations in evaporating power of air. Some animals of supposedly lower organization than the fishes, showed modifications similar in character.

II. MATERIAL AND METHOD

The following species were studied: the yellow margined milliped (*Fontaria corrugate* Wood), ground beetles (two species of *Pterostichus*), the wood frog (*Rana sylvatica* LeC.), the red backed salamander (*Plethodon cinereus Gr.*)—all from moist forest habitats; and the common toad (*Bufo lentiginosa*), the small digger wasp (*Microbembex monodonta* Say), the bronze tiger beetle (*Cicindela lecontei* Hald), and the sand spiders (*Geolycosa wrighti* Em and *pikei* Marx)—all from dry sand dunes.

The animals were put into small cages across which air was forced through three narrow slits. The ground plan of the cages is indicated in Fig. 1. The covers of the cages were of glass, the fronts opposite the slits of screen. Gradients of evaporating power were secured by passing air of different relative humidities, or different temperatures, or by passing it at different velocities across the different thirds. The device for thus controlling the rate of evaporation was designed by the writer and Prof. E. O. Deere of Bethany College. The statistical and environmental aspects of the one hundred experiments performed together with details of the methods were published elsewhere (Biol. Bull., June, 1913). Nearly seventy-five of the experiments were of such a character as to bring out the modification phenomenon. The tracings of the movements were drawn to a minute and second scale at the time of the observation (Fig. 1) and those presented here are original drafts. The different individuals could not be distinguished in a few cases, but since this error entered into all the experiments the results are constant for this piece of work. (For further discussion of this point, see Shelford and Allee, '14, p. 8).

III. EXPERIMENTAL RESULTS

To illustrate the method of obtaining and recording the data used further on, we present three charts. In Chart I, Expt. 71, the reaction of the red-backed salamander to increased evaporation in the right hand third of the experimental tank, is shown.

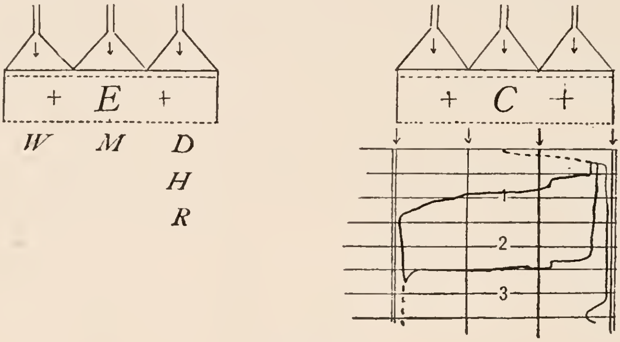


FIGURE I

Showing the ground plan of the experimental cages in their relative positions, the hood which covered and separated them is not indicated. E is the experimental cage; W, the section used for wet air; M, for the air supplied directly from the pump; D (dry), H (warm), and R (rapid flow), stand under the section where the highest rate of evaporation was maintained. The crosses indicate the positions of the 1 c.p. lights; the arrows the direction of the flow of air. The screen portions of the cage are represented by the broken lines. C, is the control cage, similar to the experimental in every way except the kind of air supplied. Below this is shown the control record of an experiment during the first three minutes. The ruling of the paper used corresponded to half minutes and the figures were written in at the center. The graph is about two-thirds natural size and the cages about one-seventh.

The increased evaporation is due to a rapid flow of ordinary air. The salamanders tried the region of highest evaporation repeatedly during the first fifteen minutes and then began to turn back when the rapid flow was encountered. We note that one individual turned back the first time it encountered the rapid flow. The control individuals came to rest practically where they were placed and moved only a little throughout the experiment.

The toads gave the same reaction to similar conditions. They tested the region of high evaporation repeatedly during the first ten minutes and then began to turn back and make short stays in that section. The control is a little less symmetrical than in most cases; for a more symmetrical control, see A, Chart IV, Expt. 42. Both species show a preference for low evaporation at the end of the period of experimentation. Chart II, Expt. 75, shows rapid modification of the behavior of the millipeds. (*Fontaria*). In the experiment, definite turnings began at the end of nine minutes, when each animal had entered the section of high evaporation. The control is a characteristic symmetrical graph for the species.

The graph of the spiders (*Geolycosa*) is difficult to interpret and is peculiar, due to the fact that the spiders are very quick and pugnacious, so that it is hardly possible for three of them to be in the same third of the cage at the same time. Still, even this graph appears to indicate what is true of single individuals namely, an avoidance of the moist and medium air. This avoidance does not begin until the end of eight minutes. The control is typical of the species and shows fairly symmetrical distribution of the spiders.

Chart III shows the reaction of the wood frog to gradients of evaporating power produced in three different ways. The graph of Experiments 60 and 70 shows the type which results from *acceleration* of *movement* or of *movement* due to mere *stimulation*. In Experiment 60, one of the frogs was placed in each third. Their commonest reaction to evaporation is to crouch close to the substratum. If, however, the evaporation continues, they finally hop, apparently at random. In the case of two of the frogs in Expt. 60, the hopping was in the direction of the lowest rate of evaporation where the frogs remained for an hour or more after the observations here graphed were ended. Experiment 70 shows first the stimulation of one frog leading to a series of hops in the direction of lower evaporating power, of another frog a little later in the direction of higher evaporating power which in turn led to stimulation, resulting in hops in the opposite direction. These graphs do not indicate modification. When compared with the next graph, where temperature was used to increase evaporating power, we note a striking difference (compare the graphs of Expts. 60 and 70 on the one hand and 73),

CHART I

Showing the modification of the behavior of the red backed salamander (Plethodon) and toad (Bufo) through a gradient of evaporation due to rapid movement of ordinary air in one section, the other two sections being supplied with respectively moist and ordinary air at the standard rate of flow (12 liters per minute, a velocity of .08 meters per second). The rapid flow was approximately .65 meters per second, or about 8 times the standard. The temperature is given in degrees centigrade. Immediately above the three columns of the ruled paper between the time scales is given the evaporation from the Livingston evaporimeters in hundredths of cc. during a period of 20 minutes immediately before and after the experiment. Distance from right to left represents the movements of the animals in the cage (lengthwise) and time is indicated by vertical distance as measured by the scales. The broken line is used where two or three animals move together. In the controls the large S's indicate that still air was used in the three sections.

CHART I

PLETHODON—AIR CURRENT 24°C — Experiment 71 Control

BUFO—AIR CURRENT—24°C — Experiment 68 Control

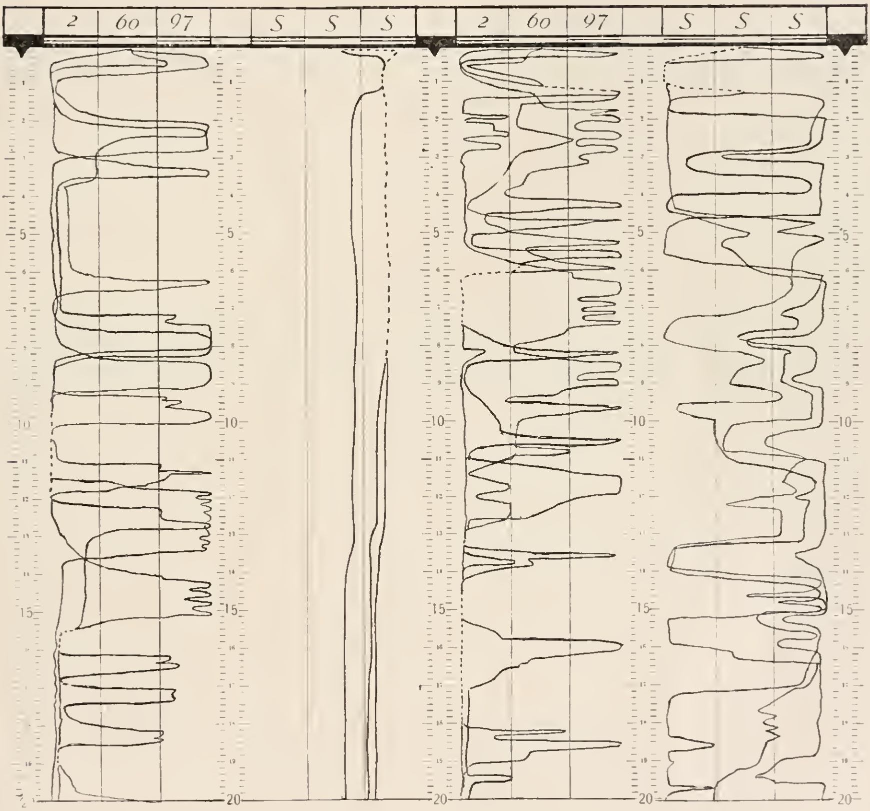


Chart II

Showing modification of the behavior of millipeds (Fontaria) and spiders (Geolycosa) through contact with an evaporation and temperature gradient. The lower temperatures given are for the left and center sections and the higher of the right hand one. For further explanation see Chart I.

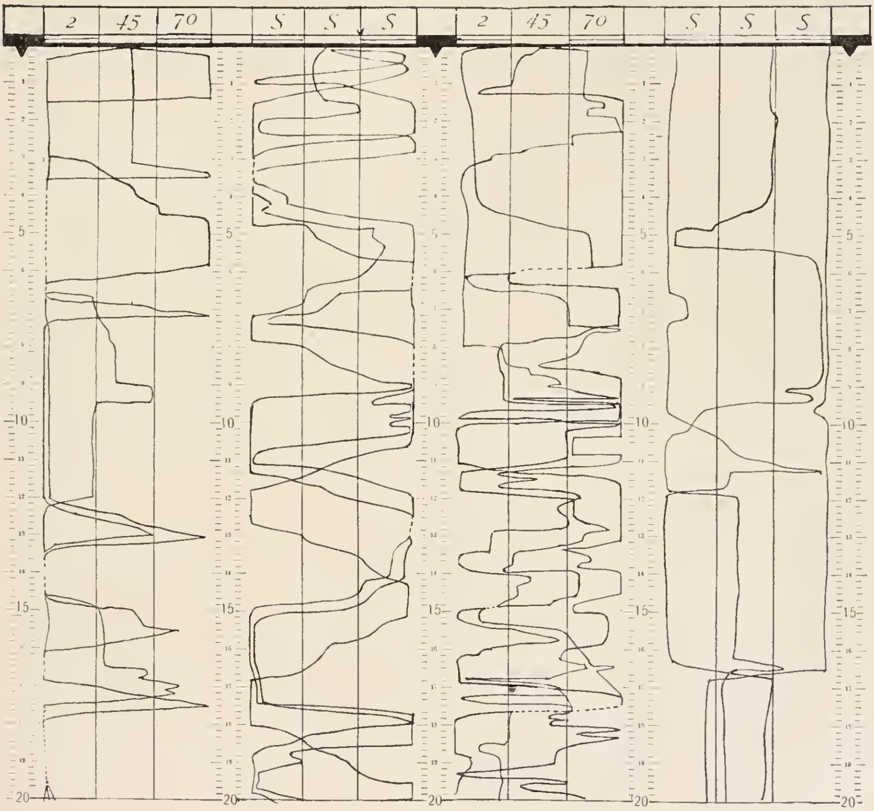
CHART II

FONTARIA—AIR TEMPERATURE
24° and 29°C

Experiment 75 Control

GEOLYCOSA—AIR TEMPERATURE
23° and 28°C

Experiment 79 Control 23°C



which is, I believe, the difference between a graph in which modification of at least one individual is indicated and one in which there is little or no evidence of modification. In Expt. 73, clearly one individual tried air of highest power, then turned back with the second trial, and repeated the same after a brief stay in the moist air. The others appear to have avoided the middle section except for one trial of the air of high evaporating power, after which all came to rest in the moist air. The control of 73, when compared with the rest of the controls indicates the greater activity which commonly occurs in the air that is moving enough to raise the evaporation above the optimum for the animals.

Evidence of modification, as in the case of the fishes (Shelford and Allee, '14), may be of the following types: (a) an animal may begin *turning back* after *entering* the stimulating air a number of times, (b) it may spend shorter and shorter periods of time in the modified air with each entrance; (c) after entering the gradient and turning back in it, an animal may begin to turn back before the change of air conditions is encountered, indicating retention; (d) after having experienced differences in one tank it may remain in one end and turn back from the other when there is no difference between the two ends. The second two types of modification may indicate learning while the first two do not.

Table 1 gives the data on these questions by species and factors. The kinds of experiments in which there was no evidence of modification, are omitted. For example, the experiments with Fontaria and wind gave no good evidence of modification and only experiments with reactions to dry and heated air are included.

Where the reactions were strongly negative the animals sometimes turned back the first time they encountered the stimulating air (Chart I, Expt. 71; Chart III, Expt. 73). All of the species, except Pterostichus which was used for only one experiment, did this when the evaporation was great. Such turnings indicate that the animals sense the strong stimulii the first time they encounter them, i.e., before their sensibility has been increased by repeated contacts with the stimulating air. We note the figures showing the number of times this happened, in the twelfth column of the table. Usually the animals showing modification entered the stimulating air a number of times before beginning

TABLE I

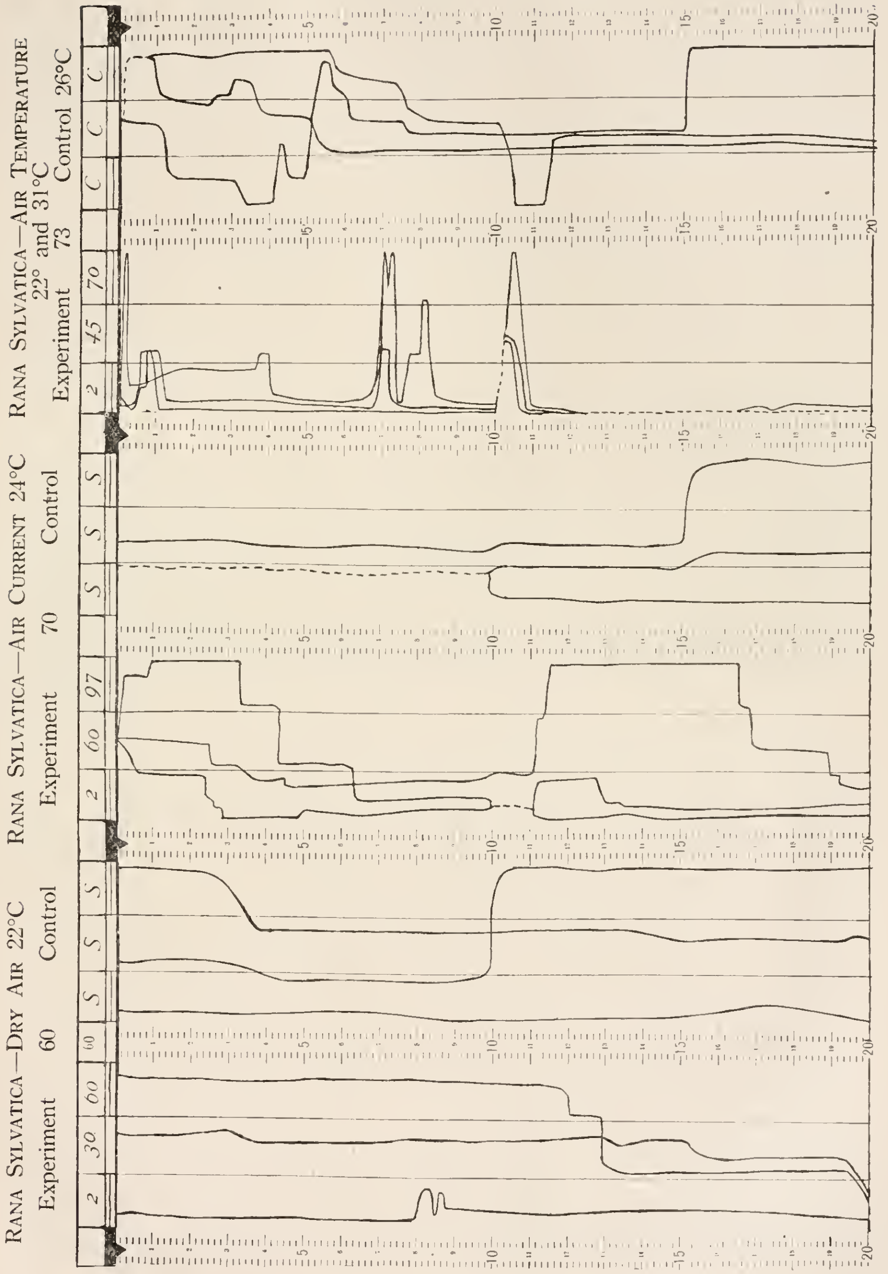
Showing the modification of behavior in the animals studied.

1	2			3	4	5	6	7	8	9	10	11	12	13	14	15
Species	Evaporation			Cause	Temperature	Temperature difference	Number of experiments	Number of individuals	Per cent of individuals showing modification	Average number of trials before modification	Average time in seconds before modification		Reaction		Control	
	L.	M.	H.								Time in lowest evaporation	Time in highest evaporation	Turned the first time	Turned before encountering gradient	Turned before encountering corresponding to gradient	Number of controls
Plethodon cinereus......	.02	.34	.58	Dry air	23	..	6	18	58	1.5	174	41	9	24	14	6
	..	.37	.71	Current	22	..	2	6	66	3.2	575	126	0	2	2	2
	.02	.35	.58	Heat	22	10	2	6	100	1.6	178	165	1	2	2	2
Averages (a) and totals (t)........................					..	..	t10	t30	a74	a2.1	a309	a111	t10	t28	t18	t10
Bufo................	.02	.34	.76	Dry air	22	..	2	6	100	1.8	338	95	2	2	1	2
	..	.42	1.01	Current	23	..	2	6	100	2.8	168	179	..	..	..	2
	.02	.45	.60	Heat	23	5 & 6	2	6	33	1.0	80	10	2	..	..	2
	.02	.22	.75	Dry air, B.	23	..	1	3	100	2.6	236	278	..	2	..	1
(Not included in totals and averages).....	.02	.22	.75	Dry air, C.	23	..	1	3	100	1.0	82	88	..	2	..	1
	..	..	..	Control, D.	23	..	..	3	100	2.0	236	230	..	..	4	..
Averages (a) and totals (t) of experiments..........					..	..	t7	21	a 82	a2.0	a205	a141	t4	t4	t1	t6
Fontaria.............	.02	.34	.73	Dry air	22	..	4	12	83	2.2	213	85	..	..	..	4
	.02	.37	.76	Heat	22	5 & 10	2	6	83	1.3	527	66	2	..	..	2
Averages (a)and totals (t)......................					..	..	t 6	t18	a 83	a1.7	a246	a75	t2	..	..	t6
Geolycosa............	.02	.32	.18	Dry air	22	..	t 4	t12	a 33	a1.5	a227	208	..	..	..	4
Pterostichus...........	.02	..	.75	Dry air	..	..	t 1	t 3	a100	a2.3	a196	26	..	3	5	1
Average of averages (a)......................					..	..	..	..	93	1.9	236	112	..	..	..	..
Total of totals (t)...........................					..	..	28	84	..	..	..	..	16	35	24	27

CHART III

Showing behavior of the wood frog (Rana sylvatica) in evaporation gradients. In the dry air and air current experiments where avoidance of the higher evaporation by stimulation and acceleration is shown. In the temperature experiment modification of reaction is indicated. In control 73 the C's indicate that the air in the control cage was moving. For further explanation see Chart I.

CHART III


RANA SYLVATICA—AIR TEMPERATURE
22° and 31°C
Experiment 73 Control 26°C
2
45
70
C
C
C
RANA SYLVATICA—AIR CURRENT 24°C
Experiment 70 Control
2
60
97
S
S
S
RANA SYLVATICA—DRY AIR 22°C
Experiment 60 Control
2
30
60
60
S
S
S
5
10
15
20

to turn back. In the ninth column, we note that the average number of such trials varies from 1 to 3.2 It will be noted, also, in the eighth column that the percent of the individuals tried, which showed modification, varied from 33 to 100. In most of the cases where no modification was indicated, the animals reacted to the higher rate of evaporation from the first or remained in the air of low evaporating power without encountering the higher; hence they do not indicate that the capacity for modification is not present under favorable conditions.

It will be further noted from the tenth and eleventh columns that the length of time spent in the air of low evaporating power is nearly always greater than the time spent in the highest evaporating power (the time spent in the central third is omitted and is usually small).

The experiments were not planned to test the ability of the animals to form associations. In the main, the work was conducted in a manner intended to prevent the formation of associations. There was a considerable stock of most of the animals and in nearly all cases the individuals used in a given experiment were not used again for some days. Still, after the gradient had been encountered a number of times, turning before it was encountered may indicate that the stimulation by the air was associated with the approach to the light or with the screen-covered side on the right (Fig. 1). In the case of *Plethodon cinereus* there were ten more turnings before the gradient was encountered than in corresponding positions in controls and with the exception of *Pterostichus*, the number of turnings in the experiment before entering the gradient exceeded that for the corresponding positions in the controls.

To test the possibility of association formation, four readings (A, B, C and D, Experiments 42 and 43, Chart IV) of the behavior of three toads were made. "A," (Chart IV) is a typical symmetrical control which was observed first. The same toads were then transferred to the experimental cage, and reading begun within five minutes. Here they began showing some avoidance of the air of the high evaporating power at the end of six to eight minutes. At the end of a twenty-minute observation, they were removed for a few (less than five) moments and then returned to the same cage (C) where they showed avoidance of the dry air in *one and two minutes*. At the end of the twenty-minute period (C), the toads were transferred (as before) to the control cage. After a few moments they began to show a preference for the same end that was preferred in the preceding period. While controls sometimes show asymmetry, this is the only one out of ten which shows any such peculiarity.

In the table, the items marked B, C, D, under Bufo, represent two experiments and the control which followed them. In the first experiment (Column 9) the number of trials before turning back was 2.6 and the time over 200 seconds in the highest and lowest evaporation. In the second experiment the trials were reduced to 1.0 and the time to a little more than 80 seconds. In the control observation which followed, they showed a preference for the end corresponding to the moist air with less trials and with less time than was required in the first experiment. Toads have no tendency to come to rest in one end, or in contact with the walls. The two sides of the cage were not exactly alike and the toads could perhaps sense the screen on their right or the lights in front when approaching the end in which the high evaporation occurred in the experiments. The one experiment suggests that the toads may have associated the lights ahead or the view through the screen with the dry air further on (see Fig. 1).

IV. INTERPRETATION OF RESULTS

Protoplasm and the plasmas of organisms possess a definite mechanism for maintaining approximate neutrality. "Neutrality is quite as definite, quite as fundamental and quite as important a characteristic of the organism as its temperature, or osmotic pressure, or in fact anything else we know" (Henderson, '13a). "Within wide limits of amount any acid or base may be poured into the organism and the reaction will not vary," nor will it vary if such be produced by the organism.

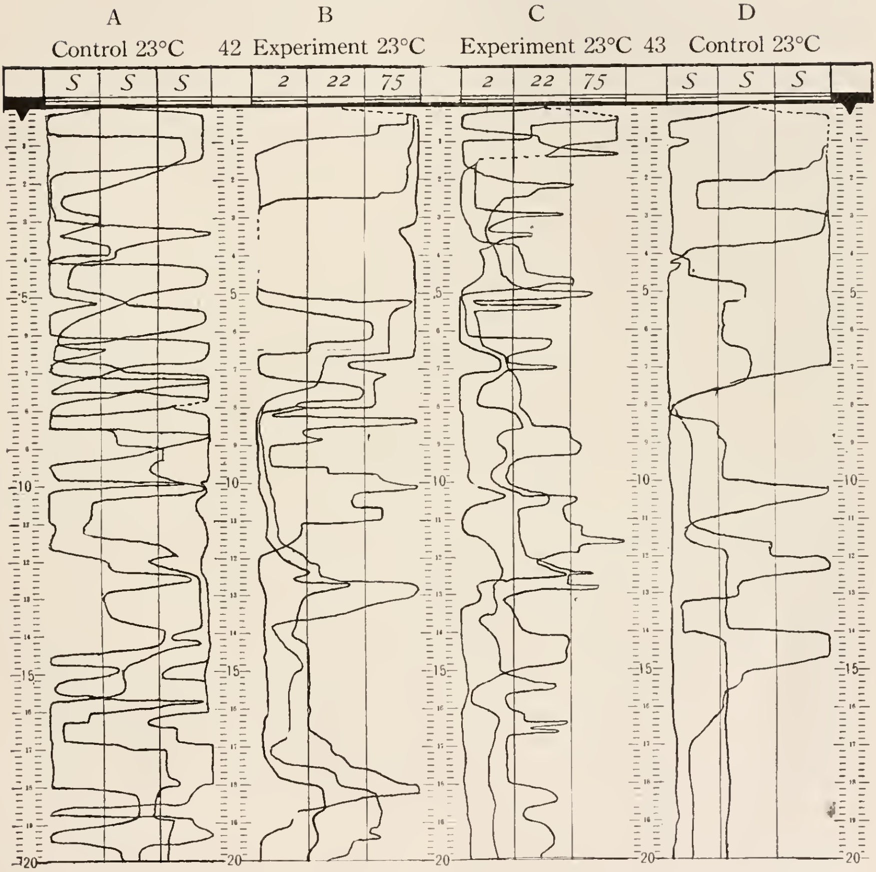
In the preceding paper we noted that presenting acid either externally or internally produced increased sensibility or increased irritability. By this we do not mean to suggest that any particular degree of acidity was probably attained except where staggering occurred, but rather that a tendency toward acidity occurred during the adjustment of the neutrality mechanism. Just what the relation of the ammonia to the neutrality mechanism is in the case of fishes and other vertebrates is not

Chart IV

Showing modification of the behavior of the toads (Bufo) as indicated by experiments following each other closely and by the actions of the toads under control conditions immediately after the second experimental reading was ended.

CHART IV

Bufo Dry Air—Possible Retention of Modification



clear, for while it doubtless causes a tendency to alkalinity, its paralyzing effects are probably due to specific action upon the protoplasm. It should be noted that alkalies, including ammonia, as well as acids, usually excite animals and are almost as potent as acids in causing reversal of reaction (Loeb, '06, Mast, '11), increased irritability, etc. It appears then that a disturbance of neutrality in either the direction of acidity or of alkalinity may be expected to give such results as we have discovered in connection with the reactions of fishes to gradients. The negative reactions here described are to conditions which can primarily either dilute or *concentrate* the *plasma* either in the peripheral sense organs or in the organism as a whole. Did this result in acidity or in alkalinity or did it disturb some other regulatory mechanism? While a probable answer to this question could be presented and discussed, we reserve it until special investigation, now about to be undertaken, may have been completed. It is, however, more than probable that the increased sensibility to air of high evaporating power is due to some disturbance of neutrality, brought about by concentration. We may note, also, that if associations are formed, they go hand in hand with and can hardly be distinguished from the other type of modification. In other words, there is no reason to assume that associative memory is essentially different or stands apart from the type of modification here described. In fact, it appears that since all excitation and all activity increase the output of carbon dioxide the neutrality mechanism may be involved in all associative processes. Henderson ('13a) says it is gradually becoming clear that all physico-chemical conditions in protoplasm—alkalinity, osmotic pressure, colloidal swelling, chemical equilibrium, temperature—are interdependent and that carbonic acid and acid base equilibrium are among all these things probably the most important variable.

Thus it seems probable that many of the simpler problems of associative memory must be referred to the biochemist for solution. The zoologist and the psychologist can by their present methods do little more than describe the phenomena of modification and the best results can come only from general cooperation. The need for cooperation between the psychologist and the naturalist is even more evident than between psychologist and biochemist.

In all of the cases here discussed, except the reactions of the wood frog to dry and moving air, and in most of the other experiments, rapid modification took place. All the stimuli used are those commonly encountered by the animals experimented upon, in their natural environments. It is impossible to determine, however, in the case of animals collected and brought into the laboratory, how much of this ability to avoid disadvantageous stimuli has been acquired during the life of the individual. We note that plants, which respond to environmental changes by variations in growth form, show a similar relation to the various stimuli. Those commonly encountered in nature usually call forth advantageous responses, while those not usually encountered call forth responses which are often decidedly disadvantageous. Here this quality could not have been acquired by the individual in its life experiences and is accordingly to be considered as an innate capacity. It is, therefore, a fairly safe assumption that the capacity to avoid disadvantageous stimuli, and the capacity for advantageous modification, are innate also. Such capacities appear to be common. The difference in the speed with which frogs learn to avoid distasteful food as compared with the time required for them to learn a maze or the presence of a glass plate is a further example of the difference between reactions to natural and unnatural stimuli and problems. As a further example, we note the difference between the apparent "stupidity" of the frog in failing to learn not to snap at a fly when the punishment was the pricking of the upper jaw by a pin or needle (Holmes, '11) as compared with the rapid learning to discriminate between the kinds of food presented when certain kinds brought punishment through the *taste organs* (Schaeffer, '11), the more usual channel for disturbing results of food taking. The raccoon is slow with a man's problem, such as a latch and door problem; what could he do with a forest and hollow tree problem the first time it was presented to him? What could a man do with a forest and hollow tree problem? That with some such problems he errs widely and loses his way often, we are well aware. The use of problems which the animals concerned could never by any possibility have encountered is legitimate, and indeed a necessity if the effect of experience is to be eliminated in animals not bred for experimental purposes. Still, is not the degree of intelligence shown by an animal, with its first problem of a kind common in the experience of the species, a better test of its intelligence in terms of what is so named in our own species, than its ability to solve an entirely unnatural problem? Why should the intelligence of a monkey be indicated any more by its ability to operate locks, than a man's, by his ability to balance himself upon the swaying branches of a tree? The comparisons may seem crude, indeed they are so, but the matter in point seems well borne out by the evidence suggested above. The error in rating the intelligence of animals *solely*, *either* upon the basis of problems which they normally encounter in *nature*, *or* those never encountered is not small. Indeed, experimental psychologists have, to a considerable degree, abandoned attempts to rate the intelligence of animals. It is still, however, a common practice among zoologists. To understand the behavior of his animals to the best advantage, the experimental psychologist, should have first-hand naturalistic knowledge of them. The naturalist is even more in need of a knowledge of experimental methods and results. It appears to one not primarily interested in either, that the experimental psychologist should be a naturalist and the naturalist an experimental psychologist.

Theoretically, the explanation of the apparent difference between the relations of animals to natural and unnatural problems is very simple. Direct evidence of recent years tends to show that *natural selection* does not usually, at least, operate upon structural characters in the manner formerly supposed. On the other hand, a rapidly increasingly body of experimental data shows that animals survive or perish under severe conditions in accordance with their irritability and other physiological characters. Irritability is the chief mechanism of survival. Accordingly, where natural selection has been able to operate, responses to stimuli are commonly advantageous; where it has not, they are often disadvantageous and sometimes clearly detrimental.

Two other points are noteworthy. The sensitiveness of the animals used, to slight differences in rate of evaporation shown, makes errors in laboratory experiments easily possible. Air current in controls were practically abandoned because some of the amphibians detected differences in the different parts of the control cage which could not be detected with the hand, making great care necessary in the preparation of each current control. The modification of behavior in gradients here discussed, has been made evident solely by the graphic method of recording the movements of the animals. It is quite possible that application of similar methods to reactions to gradients generally, may show that such modification is the rule, from the more simply organized animals upward.

ACKNOWLEDGMENTS AND BIBLIOGRAPHY

The writer is indebted to Dr. Harvey A. Carr and Mr. M. M. Wells for suggestions during the preparation of the manuscript.

All other literature consulted is cited in Shelford and Allee, '14.

HOLMES, S. J. Evolution of Animal Intelligence. Holt.
1911.

SCHAEFFER, A. A. Habit Formation in Frogs. *Jour. Animal Behavior*, Vol. I, pp.
1911. 309–335.

SHELFORD, V. E. and ALLEE, W. C. The Reactions of Fishes to Gradients of Dissolved Atmospheric Gases. *Jour. Expt. Zool.*, Vol. XIV, pp. 207–266.
1913.

SHELFORD, V. E. and ALLEE, W. C. Rapid modification of the Behavior of Fishes by Contact with Abnormal Water. *Jour. Animal Behavior*, Vol. IV, pp. 1–30.
1914.

SHELFORD, V. E. Reaction of Certain Animals to Gradients of Evaporating Power of Air, with a Method of the Establishment of Evaporation Gradients by V. E. Shelford and E. O. Deere. *Biol. Bull.* XXV, 79–120.
1913.

HENDERSON, L. A. The Regulation of Neutrality in the Animal Body. *Science N. S.*, Vol. XXXVII, pp. 389–395.
1913a.
1913. The Fitness of the Environment. New York.

LOEB, J. Dynamics of Living Matter.
1906.

MAST, S. O. Light and the Behavior of Organisms. New York.
1911.

A GRAPHIC METHOD OF RECORDING MAZE-REACTIONS

ROBERT M. YERKES AND CHESTER E. KELLOGG
From the Harvard Psychological Laboratory

One figure

For nearly twenty years the maze or labyrinth has been employed by students of animal behavior. Both apparatus and procedure have been improved steadily during the last decade, but even to-day we lack an intelligently standardized form of maze and a reliable method of recording the several important aspects of the subject's reaction.

We propose, in this paper, to describe a method of recording maze-reactions which should greatly increase the value of the results obtained in experiments with the maze. We shall not attempt to describe a type of maze which promises to be worthy of standardization, but instead shall limit ourselves to a brief discussion of methods of observation.

Experiments with the maze offer opportunities for the measuring of several aspects of reaction. Especially important among the data obtainable are (1) time of reaction; (2) distance; (3) number of errors; and (4) nature and distribution of errors. Prior to the devising of the method herein described, it has been practically impossible for even the highly practiced observer to obtain accurate measurements of all of these features of reaction. Indeed, with a rapidly moving subject like a rat or a mouse, it has been impossible, during the first few trials, to obtain with accuracy any other measurement than that of time. This is obviously quite as unnecessary as it is unfortunate, for we have good reason to believe that distance and error data are in many experiments more important than time data. Because of our conviction that a variety of data should be obtained in every maze experiment and that all measurements should be made with a reasonable degree of facility and accuracy, we have made it our business to attempt to devise a method which shall enable an experimenter to record the various aspects of reaction directly and graphically.

When the idea of using a graphic method of recording maze-reactions occurred to us, it was immediately suggested, through correspondence, to Professors J. B. Watson and Madison Bentley. The former, feeling the immediate need of such an improvement in the technique of maze experiments, promptly devised and con-

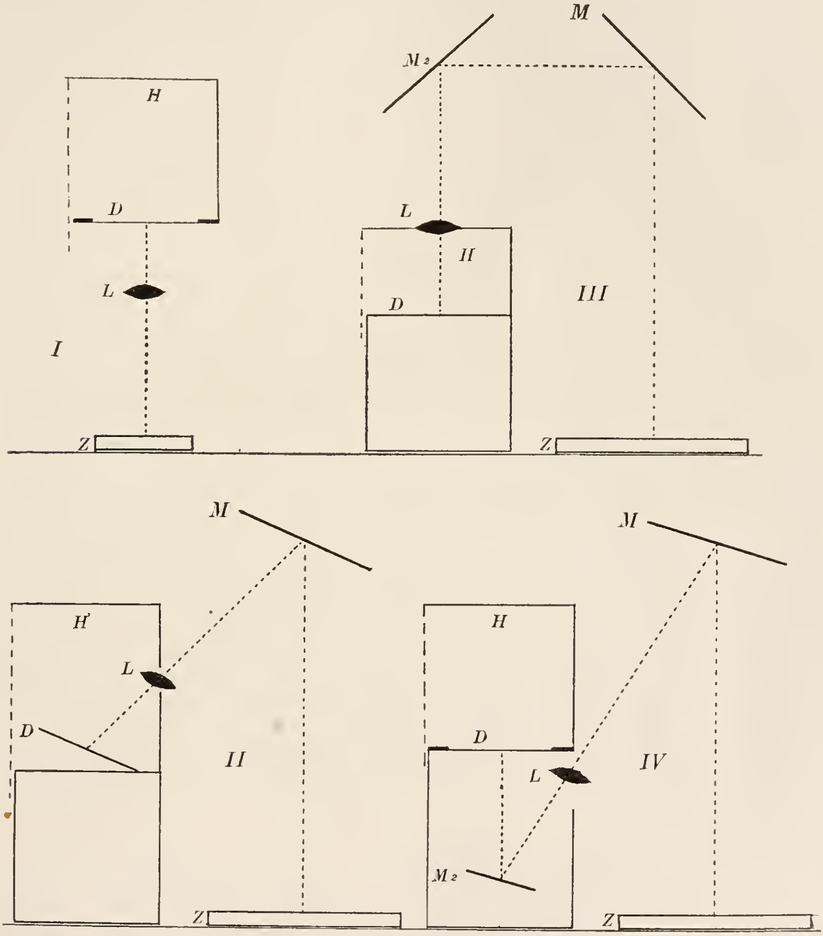


FIGURE 1

Diagrams of four types of apparatus for obtaining graphic records of maze-reactions. I. Apparatus for the direct method: Z, maze; L, lens; D, drawing surface; H, hood. II. Apparatus for simple reflection method: M, mirror. III. Apparatus for double reflection method of Watson: M and M_2, mirrors. IV. Apparatus for double reflection method of Kellogg.

structed what may be termed the camera lucida apparatus. This has been in use for several months in the Psychological laboratory of the Johns Hopkins University and is reported by Professor Watson to work satisfactorily.

In our search for simple, inexpensive, reasonably convenient and adaptable means of obtaining the desired data of reaction, we have happened upon the four methods or devices which are now to be described. Figure 1 is a diagrammatic representation of these several devices. Since they are not of precisely the same value, we shall point out the chief merits of each in describing them.

It was our aim to project, in some convenient manner, an image of the maze and of the reacting subject upon a record sheet which should bear a diagram of the maze. Upon this record sheet the experimenter may accurately trace the path of the animal, while, at the same time, keeping a record of the time of reaction. From the graphic record of the route taken by the animal, the distance and error data may be read.

We shall designate the four methods as the direct method (Fig. 1, I); the simple reflection method (Fig. 1, II); the double reflection method of Watson (Fig. 1, III); and the double reflection method of Kellogg (Fig. 1, IV).

I. *The direct method.* This is the simplest device which we have been able to imagine. Above the maze, Z, of Fig. 1, I, is placed either a simple or a compound lens, L, and at the proper distance above it, a plate of glass, D, conveniently framed in a drawing table, and enclosed by a hood, H. Upon this plate of glass, a thin sheet of paper bearing a plan of the maze is placed. As the observer looks down upon the record sheet, he sees an image of the maze and of the reacting subject, and at will he may trace with pen or pencil upon the record sheet the path followed by the subject.

This method has the important advantages of being extremely simple, inexpensive, and adaptable. It gives a reversed image of the maze, but this is no considerable disadvantage. The chief disadvantages of the method are its inconvenience in connection with large mazes because of the great distance necessary between maze and drawing board. But even with very large mazes, the method may be used to advantage if a vertical distance of twenty to thirty feet is available. This arrangement is likely to prove most practicable where two rooms, the one above the other, are available for maze experiments. The writers have tested the method only with very small mazes.

II. *The single reflection method.* The device for this method, as shown in Figure 1, II, consists of a mirror, M, which is placed above the maze, Z, and which causes an image of the maze to fall upon the lens, L. This image is focused upon a record sheet at D. As in the case of the direct method, the drawing board is hooded in order that the experimenter may work in dim light and thus be able to see, clearly, both the alleys of the maze and the moving animal. In comparison with the former method, this is somewhat more expensive. It yields a completely reversed image and it may be used for even very large mazes. Its chief defects are the inconvenient inclination of the drawing surface, at one end of which the observer must work. In this laboratory we have thoroughly tested the method and find it to work satisfactorily. A little practice enables the observer to follow a rapidly moving rat or mouse and to obtain records which yield accurate measurements of distance, time and errors, even in the early experiments with a given subject.

III. *The double reflection method of Watson (camera lucida method).* Two mirrors are used in this apparatus together with a lens and drawing board. The arrangement of these parts is shown in Fig. 1, III. This apparatus has the disadvantage of being more expensive by reason of an additional mirror than the preceding method, and it is also placed at a slight disadvantage because it supplies an image of the maze which is reversed from right to left. To counterbalance these disadvantages, we may mention the following obvious advantages: (1) the more convenient position of the drawing surface; (2) the removal of the experimenter to a considerable distance from the maze; and (3) the adaptability of the apparatus to spatial demands in room or laboratory.

A more detailed account of this method is given by Professor Watson on p. 58.

IV. *The double reflection method of Kellogg.* This differs from method III in that M_2 is placed below the lens, and the image falls upon the record sheet from below, as in method I. Disturbing shadows cast by the hand of the experimenter are thus avoided. The image obtained by this method is completely reversed and the apparatus, as a whole, is quite as adaptable as is Professor Watson's.

General discussion of methods. The above devices for obtaining graphic records of maze-reactions yield less satisfactory results than would a good photographic device, and we recommend them simply because they are less expensive in construction and operation. All are so simple that detailed description is needless. We shall, however, in concluding this article, call attention to certain important points which experience in the use of the graphic method has brought to our attention.

In the first place, although it is perfectly possible to get along with a simple lens, especially if one is working with small mazes, a much more satisfactory image may be obtained by the use of a compound lens. Second-hand portrait lenses are available and wholly suitable, but even such a lens is likely to be much more expensive than a simple lens.

Each of the four devices which we have described has its obvious advantages and disadvantages, and it is clear that choice of a method should depend upon the relative importance of these in each particular case. On the whole, it is likely to be more convenient for most experimenters to have their drawing board slightly inclined toward them. This is possible in methods III and IV. Method II necessitates the use of an inclined drawing board, but unfortunately the observer must sit at one end of this board and work in a somewhat awkward position. So far as the position of the drawing surface is concerned, methods III and IV would seem slightly more satisfactory than methods I and II.

In those devices in which the light falls upon the record sheet from above, the shadows cast by the experimenter's hand and pencil are disturbing, sometimes rendering it difficult to follow accurately a swiftly moving animal. Other things being equal, it is therefore preferable to have the light come from beneath the drawing surface, as in methods I and IV.

In the first few trials with a given animal, it is extremely important for the experimenter to be able to change record sheets quickly, since the animal is likely to traverse the alleys of the maze rapidly and repeatedly. If the image comes from above the record sheet, it is possible to have the sheets made up in the form of a tablet or block with two edges glued. The tablet having been properly oriented, the experimenter may at any moment tear off a record sheet and continue his tracing almost uninterruptedly. This method may be made to work satisfactorily even when a printed diagram of the maze appears on each record sheet, for the orientation of the block may be kept constant. When the image falls upon the record sheet from below it is necessary to use rather thin paper and to have the drawing board so arranged that the sheets fit neatly and may be quickly placed in position. Although we have tried only methods I and II in this laboratory, we are inclined to believe that it is more satisfactory on the whole to have the image come from below the record sheet. Especially in the first trials with a given animal, the time required is likely to be long, and the experimenter should be able to make his observations without undue discomfort or fatigue.

We recommend that as soon as the experimental device has been selected and properly adjusted, a zinc etching, which exactly reproduces the image of the maze as it falls upon the drawing board, be made, and that this be used in the preparation of blank record sheets. For, although a diagram of the maze is not absolutely essential, it has considerable value in connection with the early trials and sometimes prevents errors in the reading of records of later trials. It is extremely laborious and wasteful of time to draw the diagrams by hand, and if hundreds or thousands of record sheets are to be used, the cost of a zinc etching and of printing the sheets will be trivial in comparison with the value of the experimenter's time.

As appears from the above discussion, we are not in a position to recommend any one of the four methods over the others without careful consideration of the type of maze which is to be used, of the character of the lens, and the location of the apparatus. But we are fully convinced that all investigations with the maze should make use of some graphic method of recording reactions. There can be no doubt that the data previously obtained from maze experiments have only a fraction of the value which they should have, and that because of the inaccuracy and incompleteness of the records.

A CIRCULAR MAZE WITH CAMERA LUCIDA ATTACHMENT[1]

JOHN B. WATSON

The circular maze shown in Fig. 1 is made with wooden base and aluminium walls. The base is 150 cm. in diameter and 4 cm. in thickness, and is constructed as follows: Two wooden discs 150 cm. in diameter and 2 cm. in thickness are first sawed out. These two discs are finally glued together. Before glueing, however, the upper disc is marked off into a series of concentric circles. The diameter of each of the circles is as follows, beginning with the outermost one: 140 cm., 120 cm., 100 cm., 80 cm., 60 cm., 40 cm., and 20 cm. These circles are then sawed out upon a band saw. The width of the saw is so chosen that it is just equal to or slightly larger than the thickness of the aluminium sheets used for the walls. After sawing, the disc as a whole is converted naturally into a series of concentric rings. These are fastened down to the lower disc with hot glue and screws. The lower surface of the base is thus solid, while the upper surface shows a series of grooves into which the aluminium walls may be slid. Soft aluminium bought in rolls is used for the latter. The height of the aluminium is 18.5 cm., the thickness, .8 mm. The aluminium is unrolled and cut into the proper lengths. Each strip is cut just 10 cm. shorter than the length of the circular groove into which it is to be fitted. This gives an opening into the alley. By means of this arrangement it is possible to slide the aluminium around in its groove and thus to place the entrance in any desired position. Fig. 1 shows clearly the construction of the maze, the number of alleys, the placing of the entrances, and the radial stops.[2]

This maze offers several desirable things in work of this character: in the first place it can be used on the unit plan, in that only the home box and the surrounding segments need be

---

[1] From the Psychological Laboratory of The Johns Hopkins University.

[2] The base as a whole may then be sawed into half or quarter sections for convenience in shipping or storing. Indeed, it is easier to build the base in half sections. When set up the sections are locked together and placed horizontally upon a wooden framework. The material should be well seasoned. A thorough coating of boiled linseed oil should be applied.

used where a very simple maze is desired. The addition of other segments then merely increases the complexity in an, at present, unknown ratio. The coefficient of increasing complexity could be determined by allowing one group of animals to learn the maze in its simplest form, another in its next most complex, etc.

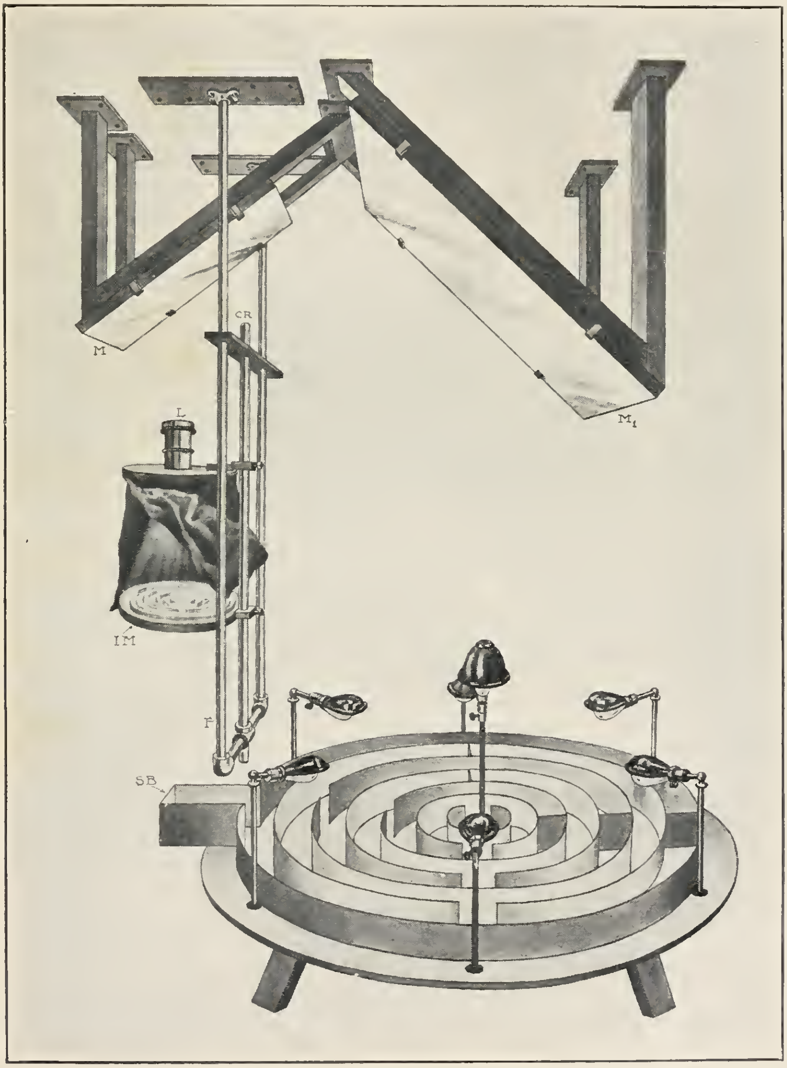


FIGURE 1. General view illustrating camera-lucida maze

Secondly, the ease with which complications can be introduced makes the maze very desirable. This is brought about by the flexibility in the arrangement of the entrances and radial stops. Fig. 1 shows the maze just as it was used by Miss Hubbert in the work which she reports on page 60.

The camera lucida attachment is easily installed; it is simple and permanent. Had it not been for Professor Yerkes' insistence upon the necessity for having some recording device for the movements of the animals, it is doubtful if this attachment would have been made in its present form. He suggested to me two years ago that some such device would be desirable and that he had certain plans for its construction. Before the publication of his work it became necessary to have an exact record of the stages of the acquisition of the maze habit, since Miss Hubbert wished to undertake a comprehensive study of the difference in the acquisition of habits of animals of different ages. Accordingly, I went ahead independently and finally constructed the apparatus which is shown in Fig. 1.

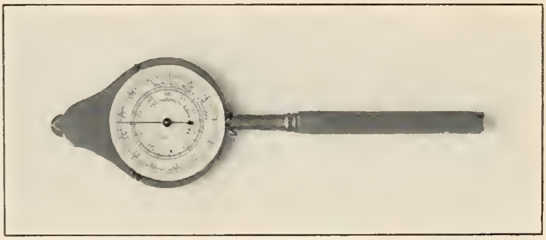


FIGURE 2. Chartometer

A large plate glass mirror (M_1), 91 cm. wide by 121 cm. in length, was placed at an angle of 45° directly over the center of the maze. This mirror was strapped by small clamps to the edge of the supporting framework. At a certain distance from this mirror a second mirror (M), 60 cm. by 75 cm., is placed at an angle of 45° above the maze and at such a distance from M_1 that the light reflected downward from M falls outside of the maze. Below M, and in the path of the light reflected from it, is placed a single achromat (L), 6 cm. in diameter and 50 cm. focus. The lens is placed in a barrel and the barrel is attached to a wooden disc 30 cm. in diameter. This board is attached to an iron collar which slides freely up and down the rod CR. This gives a very easy means of adjusting the size of the image, focusing, etc. Below this first disc will be found a second disc similar in character and controlled in the same way. A pad of circular paper is laid upon this disc.[3] A reduced image (IM) of the maze appears upon this paper. Extraneous light is excluded by means of a soft black flannel curtain attached to the disc which supports the lens (L). As may readily be seen from the figure, the maze must be illuminated quite highly in order to produce a clear image. The illumination is obtained by means of six lights placed symmetrically around the maze and by one light in the center of the maze. The six lights on the periphery are supplied with opaque half shades, the light in the center of the maze with a similar opaque circular shade. These shades are of aluminium, blackened on the upper surface. The floor of the maze is covered with imported white linoleum. This serves to reflect the light upward to M_1, thence to M. Passing through the lens the rays are brought to a focus at IM. The ratio between the maze and the image is 6.4 to 1. The image appearing at IM is extremely clear when proper precautions are used to sensitize the eye. Even the smallest mouse can be seen quite clearly.

The movements of the animal are traced upon white paper with a soft pencil. In the early stages of learning several sheets of paper are used on each animal at any given trial in order to avoid a too complicated tracing. Each sheet is marked with the number of the animal, the number of the trial and the serial number of the tracing. The length of the lines so traced is measured by means of a chartometer furnished by Eugene Dietzgen and Co. Keuffel and Esser furnish a similar and somewhat better instrument. This instrument is surprisingly accurate even in measuring lines which are tortuous in their course. The error in measuring the length of the charted lines is about one per cent. Fig. 2 shows the chartometer actually employed.

---

[3] It is convenient to cut out several sheets upon a disc cutter and to stamp a hole 13 mm. in diameter in the center of each for the reception of a stud 13 mm. in diameter and 1 cm. height placed in the center of the board IM.

TIME VERSUS DISTANCE IN LEARNING[1]

HELEN B. HUBBERT

The present investigation is concerned with the factors of the total time consumed and the total distance run in the learning of the maze by rats. The maze used in obtaining the records presented below was designed by Professor Watson. He describes the maze elsewhere in this issue of the Journal (p. 56).

The records were taken in terms of the time consumed in running from the point of entrance to the food box, and of the total distance traversed during this time. Timing was done by means of a continuous stop-watch registering one-fifth seconds. The watch was started the moment the animal left the starting box (S. B., Fig. 1, p. 57) and was stopped at the moment of entrance into the food box in the central compartment of the maze. The distance record was obtained by tracing the movements of the rat upon soft white paper with a very soft pencil. The tracing so obtained was then measured by means of a chartometer which had been calibrated. Calibration showed that the instrument had an error of about one per cent. As has been stated by Professor Watson, the ratio of the size of the image to that of the maze is as 1 to 6.4. Consequently, the distance in cm. obtained with the chartometer must be multiplied by 6.4 in order to obtain the actual distance run by the animal. The values given in the table represent the actual distance covered by the rats. For example, in trial 31 (p. 163), the distance accumulated by the chartometer was 92.69 cm. Converting this we have 92.69 cm. x 6.4=593.2 cm., as the actual distance run. Figure 2 shows the actual tracing, figures 1 and 3 the diagrammatic representation, of the paths traversed by two rats in the trials indicated.

The records of the total time consumed (T.) and of the total distance (D.) run were taken on 27 rats, 14 males and 13 females. The animals began the problem when 35 days old. They were born and reared in the laboratory, consequently all were tame and accustomed to handling. The rats had been fed in the maze

---

[1] From the Psychological Laboratory of the Johns Hopkins University.

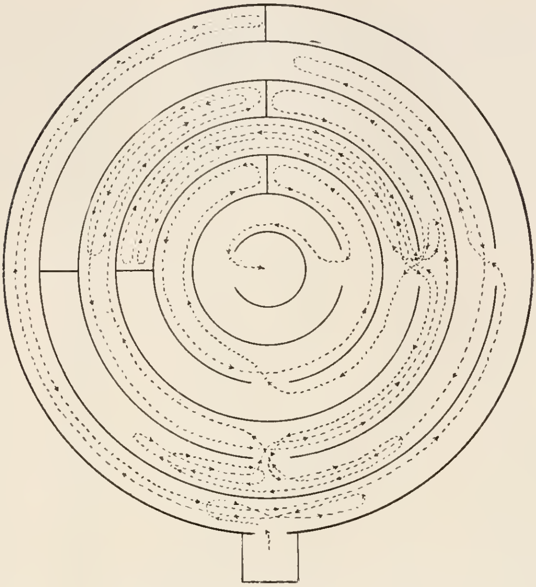


Figure 1. Schematic representation of pathway traversed by rat No. 28 on his 2nd trial in the maze. Four sheets were used in the actual tracing. Time, 2419.8 seconds. Distance, 1579.2 cm.

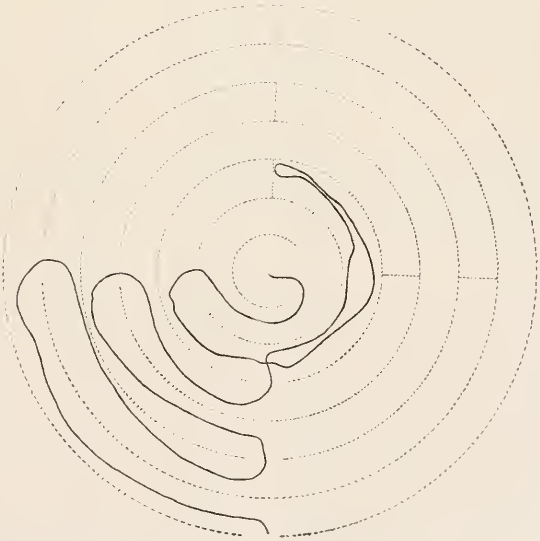


Figure 2. Actual pathway traversed by rat No. 26 on the 62nd trial in the maze. Time, 31 seconds; Distance, 630.4 cm.

for a week before the experiment began, but during feeding they were strictly confined to the food box.

Two trials per day were given each rat, and at the end of the second trial the animal was allowed to eat in the food box for from three to five minutes. Milk-soaked bread was used as the incentive throughout. Until the animals were 45 days old they were allowed to eat food in the cage for from three-quarters of an hour to one hour after each day's run. The rats were run every day and as nearly as possible at the same hour every day, since it was found that rats accustomed to being run at night did not react well if forced to run in the daytime.

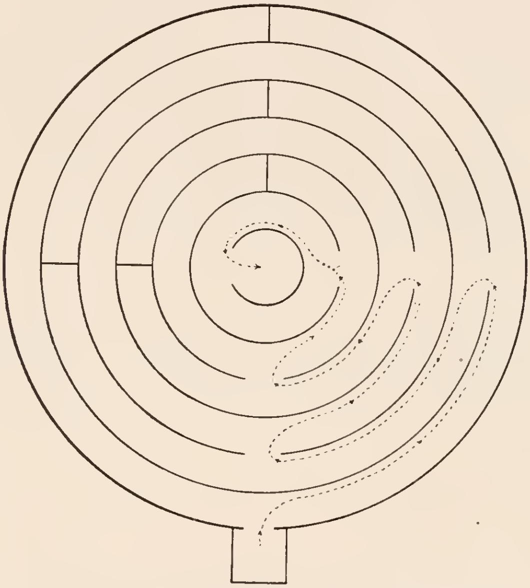


FIGURE 3. Schematic representation of pathway traversed by rat No. 26 on the 78th trial in the maze.
Time, 5.8 seconds. Distance 448 cm.

The problem was considered learned when the rat, for six consecutive trials, went straight to the food box without stopping or turning aside from the true pathway, i.e., when all excess movements had been eliminated. No time limit was set, but as a matter of fact it was found that most of the rats made such runs in six seconds or less. The shortest perfect run was 4.2 seconds,

TABLE 1

Trial No.	No. Rats Running	Average Time	Average Distance cm.	Trial No.	No. Rats Running	Average Time	Average Distance cm.
1	27	467.0	4216.1	59	18	15.9	607.7
2	27	627.7	3736.1	60	18	10.6	550.9
3	27	413.8	3147.8	61	18	10.1	519.5
4	27	158.5	1866.9	62	18	9.9	558.0
5	27	129.9	1573.6	63	18	14.5	553.5
6	27	186.6	1719.2	64	18	12.9	581.3
7	27	79.2	1164.1	65	18	10.1	551.7
8	27	68.8	1300.2	66	17	8.4	518.2
9	27	48.1	925.6	67	16	10.5	562.2
10	27	64.9	1169.0	68	16	8.8	505.0
11	27	40.3	1029.8	69	16	6.6	473.4
12	27	62.9	1240.7	70	16	22.5	496.6
13	27	59.4	925.1	71	15	7.7	484.3
14	27	77.7	1022.5	72	15	8.4	489.4
15	27	86.9	874.6	73	15	8.7	518.0
16	27	25.5	868.4	74	14	18.4	519.3
17	27	20.8	671.5	75	11	12.9	416.0
18	27	51.0	1148.1	76	10	26.5	526.7
19	27	33.1	772.0	77	8	11.2	480.8
20	27	35.4	1032.7	78	6	44.6	706.1
21	27	24.2	739.9	79	5	42.3	798.7
22	27	48.2	1010.4	80	5	36.4	508.2
23	27	19.6	649.5	81	5	8.6	448.0
24	27	24.5	789.0	82	5	147.7	788.5
25	27	27.7	754.7	83	4	28.1	600.0
26	27	26.1	756.5	84	4	359.8	1468.8
27	27	71.6	776.6	85	4	55.9	794.4
28	27	16.9	633.3	86	4	6.6	451.2
29	27	36.7	641.9	87	4	19.7	513.6
30	27	25.1	790.8	88	4	6.3	448.0
31	27	31.8	593.2	89	4	13.9	556.8
32	26	25.1	734.8	90	4	7.4	526.4
33	25	100.5	830.5	91	3	47.7	780.8
34	25	30.3	821.6	92	3	15.8	669.9
35	25	19.6	559.5	93	3	24.1	805.3
36	25	31.2	840.5	94	3	6.1	448.0
37	25	19.9	520.6	95	3	52.2	1339.7
38	25	20.5	674.1	96	3	7.2	509.9
39	25	27.3	569.6	97	3	24.7	904.5
40	25	28.9	879.7	98	3	7.0	448.0
41	25	57.3	704.0	99	3	10.1	460.8
42	25	18.2	616.7	100	3	6.1	460.8
43	25	9.0	505.0	101	3	6.9	448.0
44	25	13.7	603.8	102	3	5.3	448.0
45	25	12.3	497.5	103	1	11.2	448.0
46	24	19.0	716.4	104	1	5.4	448.0
47	23	37.1	683.4	105	1	8.0	537.6
48	23	14.7	574.3	106	1	4.8	448.0
49	22	24.1	581.2	107	1	8.0	448.0
50	22	24.4	706.5	108	1	12.0	566.4
51	21	15.7	534.3	109	1	5.2	448.0
52	21	12.6	514.7	110	1	5.4	512.0
53	20	14.1	521.6	111	1	5.4	448.0
54	20	9.9	500.8	112	1	5.2	448.0
55	19	8.4	506.8	113	1	4.2	448.0
56	19	13.3	545.2	114	1	4.8	448.0
57	19	19.6	588.3	115	1	5.8	448.0
58	19	10.4	562.5	116	1	4.0	448.0

the longest, 14.2 If a rat remained in the maze for 15 minutes without reaching the food box he was taken out and replaced in the entrance box for a second attempt. Distance and time were recorded in the same way as for a successful run, i.e., when an animal worked for 15 minutes on his first trial, and failed, and then attained success after eight minutes on his second attempt, the total time of his first trial would be 23 minutes. Distance was treated in a similar way.

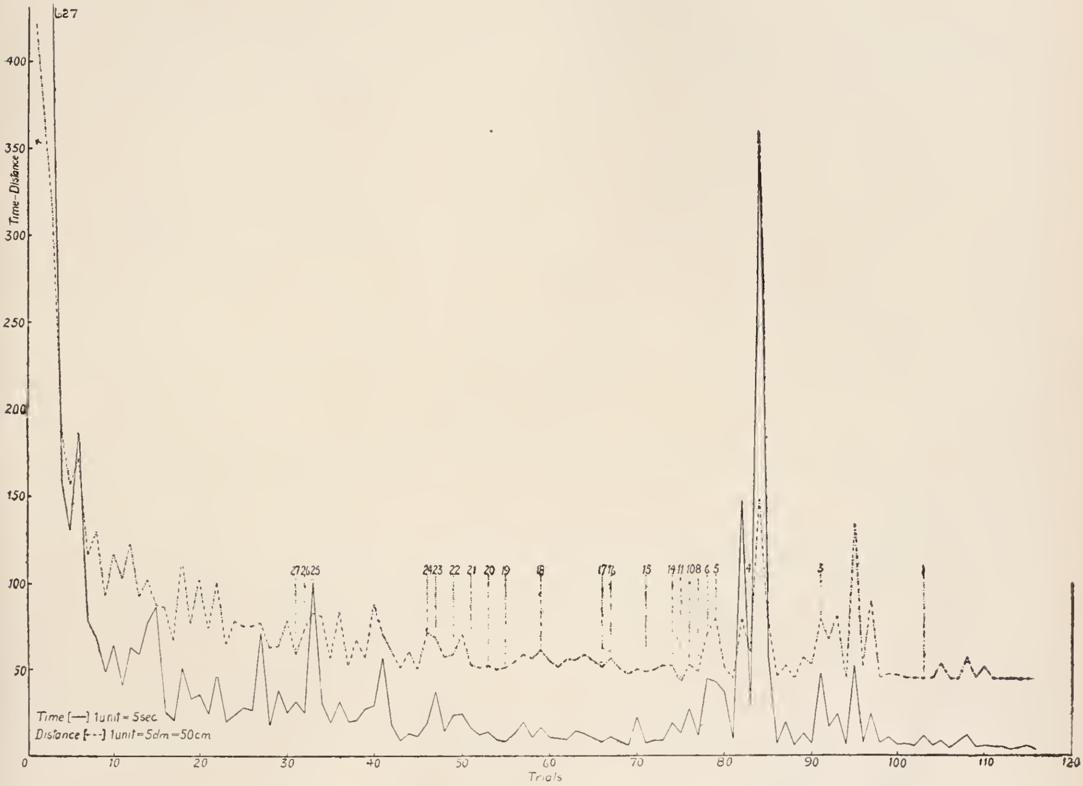
In the Table 1 given above, the time record and distance record of all individuals at work upon the problem at any given trial were separately averaged, e.g., in trial 1, 27 animals were used, the time and distance records were taken and then averaged separately, giving one point on the time curve and one on the distance curve respectively. Once the problem had been learned by an animal it was taken from the group. As may be seen in Curve 1, plotted from Table 1, the number of animals at work is steadily decreasing.

The striking similarity between the time and distance curves bears out the contention of Watson and of Hicks that the time record is a good index of progress in learning. It will be recalled that this position has been severely criticised by Washburn[2] and by Yerkes[3]. The similarity of the curve contour, and the close correspondence of the maxima and minima is apparent. As Hicks has pointed out, certain differences between T. and D. appear in the early trials. The drop in time in the first nine trials is 89.5 per cent, while that in distance is 78.5 per cent. A partial explanation for the increased percentage of the time drop may be found in the rat's behavior during the first few runs in the maze, when he often crouches against some partition and refuses to run for three, six, ten and sometimes even fifteen minutes. In such cases the *time* average increases enormously, while the distance average remains practically unchanged. Perhaps a better method of procedure would have been to deduct from the time record the time spent in absolute quiet, but this would lead into difficulties of standardization, making necessary an arbitrary decision as to how much time shall elapse without movement on the part of the rat before deduction is justifiable—a pitfall similar to that encountered in computing *errors*, and one we are anxious to avoid. It is this same system of taking records, however, which largely accounts for the apparent discrepancy in the time curve from the 81st to the 86th trial. Rat No. 22 became erratic, increasing his time record enormously here, while his distance record changed but little. Thus in the

---

[2] Washburn, M. F., *Jour. Comp. Neur. and Psy.*, 1907, Vol. 17, p. 532.

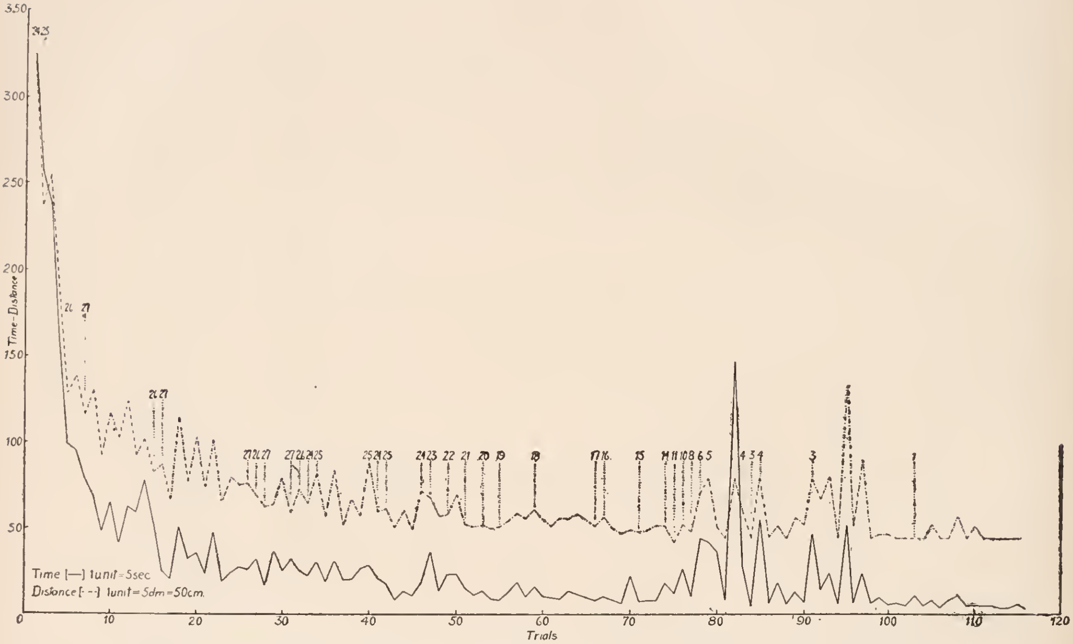
[3] Yerkes, Robert M., *Jour Phil., Psy. and Sci. Methods*, Vol. IV, p. 585..



CURVE I. Relation of time to distance. The figures above the curve indicate the number of rats running at each trial. Failures are counted in. The first point in the time curve is 350, the second (not shown in curve) 627. Plotted from the figures in Table 1.

82nd trial, where the first decided rise occurs, his time record was 715 seconds, while the combined time of the other rats running was only 23.6 seconds. Had No. 22 not been running the average time would have been 5.9 seconds instead of 147.7 seconds, while the average distance would have been 448 cm.

instead of 788.5 cm.[4] So in the 84th trial. Here the recorder's note-book states that after the first spurt, which occupied a little over two minutes, the same rat, No. 22, refused to run and crouched near the far partition in alley 1 for the remainder of the 15-minute norm. Again throwing out his record, we have a time average of 5.3 seconds instead of 359.8 seconds and a distance average of 4,480 cm., instead of 1,468 cm. In the 86th trial, he steadied down and the throwing out of the record here gives 5.4 seconds instead of 6.6 for time and 452.3 cm. instead of 45.1 cm. for distance. The small curve, Curve III, shows the effect of throwing out the record of rat No. 22. The similarity of the time and distance curves again becomes apparent. An additional factor which must be considered in respect to both time and distance, when interpreting the latter part of Curves I and II, is the small number of rats then running. The best ones had dropped out



CURVE II. Plotted from Table 2, which is the same as Table 1, except that failures are eliminated.

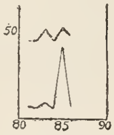
---

[4] It will be remembered that the minimum time may be taken as seven seconds while the minimum distance is 448 cm.

and at the 81st trial only five were running, while at the 86th trial only four remained. Where only a few animals are running individual differences are sure to alter the curve contour.

With the exception of the discrepancy shown in the first eight trials and the apparent discrepancy in the final trials, the time and distance curves show great similarity in contour.

Table 2 shows the effect of throwing out both time and distance records in each case of *failure* on the part of individual animals. It was found that the figures were identical with those of Table 1, except for the trials indicated. For the sake of comparison the original records (Table 1) for the corresponding trials are repeated. Examination of Curve II, plotted from these figures, shows a somewhat steadier curve and in general a closer approximation between time and distance. The same explanation which was offered in the case of Curve I for the discrepancy from the 81st to the 86th trial holds here.



CURVE III. To show the effect of eliminating the records of Rat No. 22 from the 81st to the 86th trial.

TABLE 2

Trial No.	Failures Averaged			Failures Eliminated		
	No. Rats	Average Time	Average Distance cm.	No. Rats	Average Time	Average Distance cm.
1	27	467.0	4216.1	24	325.7	3203.2
2	27	627.7	3736.1	25	257.1	2373.9
3	27	413.8	3147.8	25	236.9	2553.7
5	27	129.9	1573.6	26	98.4	1279.7
6	27	186.6	1719.2	26	95.3	1379.7
15	27	86.9	874.6	26	53.3	822.7
27	27	71.6	776.6	26	32.4	700.5
33	25	100.5	830.5	24	23.0	648.0
41	25	57.3	704.0	24	20.3	595.1
84	4	359.8	1468.8	3	5.3	448.0

In an admirable discussion of the values of curves of learning[5] Miss Hicks says (p. 141): "The total distance criterion presents so many difficulties as to render it impracticable for ordinary work. One difficulty lies in the matter of taking records accurately. The rats, after a few trials, run so rapidly that it is extremely difficult for one person to observe and record at the same time. To do this, it is necessary to mark off the maze into small segments and commit to memory some scheme of representation so that records can be jotted down in a purely automatic manner. The work of transcribing this record into distance terms and computing the same is very laborious. *Eliminating these practical difficulties, the distance criterion is in some ways an ideal one.* (Italics mine.) There can be no divergence of practice as to what shall be omitted or included and results obtained by different experiments upon the same maze will be strictly comparable." (Page 154.) "The distance and error criteria are fundamentally alike. The distance curve is the better representative of the progressive approximation of the act towards automatic accuracy. It portrays all the details of this eliminative process and it approximates the ideal of uniformity and regularity of descent. However, it is impracticable from the standpoint of recording and manipulating the data."

These practical difficulties in recording and manipulating the data have been overcome, at least where small animals are the subjects used in the maze. The total distance record can be obtained accurately. Its desirability has, so far as we know, never been questioned. The error curve has often been used in lieu of the distance curve, but it has been criticized as practically valueless because of the difficulties encountered in standardizing an "error."[6] "The prevalent practice of omitting all total and partial returns from the error record, and of making no attempt to evaluate varying degrees of error gives a curve which is not only worthless but false."[7]

With this criticism on the customary methods of obtaining the errors committed by an animal we are in hearty sympathy. It is far better, both from the standpoint of convenience and that of accuracy, to base comparisons upon the time alone than to consider these so-called errors. As to which type of record is best, time or distance, it seems wise to await a more complete study of the question before deciding.

---

[5] Hicks, V. C., The relative values of the different curves in learning. *Jour. Animal Behav.*, Vol. 1, pp. 138–156.

[6] Watson J. B., The behavior of noddy and sooty terns. *Carnegie Pub.*, No. 103, p. 249, note 1.

[7] Hicks. Ibid., p. 156.

CONCLUSIONS

I. It is possible to chart the path of the run of an animal through the maze and to measure accurately the total distance covered in that run.

II. Time and distance curves are so similar in character when normal animals are tested that it is impossible to state which is the better criterion of learning. We are sadly in need of a close analysis of just what time and distance curves mean. In determining the activity at different ages, the difference between blind and normal animals, between anosmic and normal animals, etc., there still remains the possibility that the distance and time curves will show great disparity. It is not fair, however, to maintain this until there is some factual evidence in its favor.

ON SOUND DISCRIMINATION BY CATS

W. T. SHEPHERD, Ph.D.,
Waynesburg College

This paper is a report of experiments which were made on cats, to ascertain their ability to discriminate sounds; viz.: differences of musical notes of different pitch, and differences of intensities of " noise." If an animal forms an association between a certain musical note and food, so that he reacts in a definite manner to that note in order to obtain food, and does not so react to other notes, we may infer that he discriminates that note from the other notes. In a similar manner a cat may give evidence that it distinguishes one " noise " from another " noise " of a different intensity.

Kalischer[1] has reported experiments with dogs on auditory discrimination, in which his animals showed ability to discriminate pitch. His method was to sound a certain note on an organ, or on an harmonium, whereat the dog should react in a definite manner, such as by springing up and snapping at a piece of meat which the experimenter held out in his hand. Selionyi,[2] using the " Pawlow method " on dogs, obtained evidence of discrimination by them of the tones of an organ, of organ pipes, and of the sounds of two whistles. Selionyi, as well as Kalischer, was chiefly interested in sound discrimination from a physiological standpoint. In experiments on auditory discrimination in raccoons made by the present writer, reported by Cole,[3] evidence of discrimination of musical pitch by these animals was obtained. In experiments which I made in 1909 on auditory discrimination in Rhesus monkeys, satisfactory evidence of discrimination by the latter animals of pitch, and also of " noise," was obtained.[4] Johnson,[5] in tests on sound discrimination in dogs, lately made at the Johns Hopkins University, got some positive results. However, I am informed in a verbal report of the experiments by Dr. J. B. Watson, that an average of only about 60 per cent. of correct responses was obtained.

---

[1] Kalischer, O., Eine neue Horprufungsmethode bei Hunden. *Sitz. d. Kgl. Ak. d. Wiss.*, X, 1907, 204 ff.

[2] Selionyi, G. P., Contribution to the study of the reactions of the dog to auditory stimuli. St. Petersburg, 1907.

[3] Cole, L. W., Concerning the intelligence of raccoons. *Jour. Comp. Neur. and Psy.*, **17**: 236.

[4] Shepherd, W. T., Some Mental Processes of the Rhesus Monkey. *Psy. Rev.* Mon. Sup. No. 52, 1910, 26 ff.

[5] Not published at this writing, Dec. 17, 1912.

At the time the experiments herein reported were begun, one of the animals was eighteen months old. Its only previous training had been in some tests on discrimination of articulate sounds, completed about nine months previously to those experiments. The animal appeared to be of medium intelligence. The other cat, the mother of the first, was about four years old. It had received the same training in sound discrimination as the other animal, and at the same time. The latter cat was of average intelligence. Both were ordinary grey house cats.

In the experiments on pitch discrimination to be reported in this paper, I used the same plan as I had employed in the experiments with the raccoons and with the monkeys, and which is somewhat similar to the method Kalischer employed. The cat was placed in a cage 66 centimeters in height. A wire netting formed the front, and also the top of the cage. The experimenter sat at a distance of about a meter from the cage and sounded a certain note on the instrument used. At this note, in the case of the first animal, Pet, the cat was to rear up with its paws on the front of the cage and look up through the top of the cage for food to be given it. At the other notes, it was not so to react. In the case of the second animal, Mary, on account of its inactive habits, as shown in previous experiments, it was deemed a sufficient response if it merely looked up at the top of the cage for food, when the "feed" note was sounded. But whether or not a positive response was obtained, the animals were fed when the "feed" note was sounded. Ten seconds were allowed for a response. In experiments 1 and 2, an ordinary harmonica, A, was used; in experiment 3, a Bradbury piano; the procedure in experiment 4 will be explained under that head. In each test, care was taken not to give by looks, movements of the hands, or in any other manner, any cue to the proper response. In order that the animal might not react to the mere rhythm of the sounds, they were sounded in an irregular order.

1. Discrimination of a Difference of Two Octaves of Pitch on a Harmonica. A-3, Food Note; A-1, Non-food Note.

Pet.—In the first day's experiment, this animal showed indications of forming the association; in thirty trials[6] it responded to A-3, the food-note, fourteen times, and to A-1 two times. Its first correct reaction was in the eleventh trial, the next in the twelfth, next the fourteenth, then the seventeenth, and in an increasing degree throughout that day's tests. On the second day, in fifteen trials, or in forty-five trials in all, Pet had perfected the association. In fifteen trials on that day it responded to A-3 fourteen times with one doubtful response, and to A-1 one time with three doubtful. In two trials that day, the fourth and the seventh, the animal got up at A-1, but got down at once and appeared, from its looks and actions to know that it had made a mistake. In ten test trials four days later, the cat reacted to A-3 ten times and to A-1 none.

Mary.—The older animal showed no definite indication of forming the association until the third day. On that day, in ten trials, it responded to A-3 eight times and to A-1 five times with two doubtful responses. After this, Mary continued to improve, and on the seventh day had perfected the association. In twenty trials that day, or in ninety trials in all, the animal responded to A-3 nineteen times, and to A-1, five times, with two doubtful. At the twentieth trial, when I sounded A-1, Mary went to " washing her feet," and appeared, by her actions, to know that no food was to be gotten at that note. In two additional day's tests, Mary responded to A-3 twenty times in twenty trials each day, with five and four wrong responses respectively on the eighth and ninth days. This cat never entirely inhibited the tendency to react to A-1.

2. Discrimination of a Difference of One Octave of Pitch. Notes A-2 and A-1 on a Harmonica. Fed at A-2.

Pet.—In the first day's experiment, in ten trials, the animal gave no positive response. I had handled it rather roughly on the previous day, and the cat appeared uneasy and afraid of me. Also it did not seem hungry. On the following day, in twenty trials, or in thirty trials in all, Pet reacted to A-2 eighteen times and to A-1 two times. It did not respond to A-2 in the first trial nor in the eleventh. The animal reacted to A-1 (wrong) in the third and fifth trials only. When it got up at A-1 in the fifth trial, it *got down at once*, and gave every indication of being aware that it had made a mistake. In a test of ten trials on the following day, Pet made no mistakes.

---

[6] That is in thirty trials of each auditory stimulus.

3. Discrimination of the Difference of Two Octaves of Pitch on a Piano; i.e., between F-1, Bass Cleff, and F-2, Treble Cleff. Fed at F-1. Not fed at F-2.

Pet.—On the first day of this experiment, in twenty trials, the cat reacted to A-1 thirteen times and to A-2 three times. Its wrong responses to A-2, were in the first, second and fifteenth trials. On the second day of the experiment (three days later), in twenty trials, or with forty trials in all, Pet responded to A-1 twenty times and to A-2 none. In the first trial on that day, the animal got up *slowly* at the food-note, as if in some doubt what to do. In the remaining nineteen trials correct responses by the cat were prompt.

4. Discrimination of Noise.

The animal was placed in the cage as in the preceding experiments on pitch discrimination. The sound apparatus consisted of a wooden box, 18 x 11 x 10 inches, and a slat 13 x 4 x $\frac{5}{12}$ inches, fastened to the top of the box by a leather hinge. By raising the free end of the slat and suddenly letting it go, it struck the top of the box and made a sound varying in loudness with the force with which it struck. To give sounds of different degrees of intensity or loudness, two sticks, one 2½ inches in length, the other 4½ inches, were separately used and placed perpendicular to the box, under the free end of the slat. By pressing on the slat near the hinge and suddenly removing the shorter stick, the slat would strike the box and produce a sound of noticeable intensity, and by using the longer stick in a similar manner, a louder noise was made. The same pressure, as nearly as possible, was exerted on the slat in both cases. By rearing up and looking through the top of the cage when the louder noise was made, the animal was to show its discrimination of the louder and lesser noises. It was fed at the louder noise and not fed at the lesser. The noise apparatus was manipulated at the closed side of the cage, so it was not possible the reactions were to stimuli other than the sounds. The noises were made in an irregular order.

Pet.—On the first day of the experiment, in twenty trials, the animal reacted to the food-sound, the louder noise, eight times, to the lesser noise four times and with three doubtful responses.

In the third trial (the first correct response), in the eighth and in the fifteenth, though giving the correct response to the stimulus, the cat's reactions were slow, as if in some doubt what to do. On the second day, in twenty trials, or forty trials in all, Pet reacted to the louder noise twenty times and to the lesser noise none. In the second and fourth trials it *started* to respond to the lesser noise *but stopped.* On the next day, being tested in fifteen trials, the animal made no mistakes.

We may regard the results of these experiments as positive. In the experiments on pitch discrimination, the criticism may be offered that the experimenter should have sounded the notes out of the animal's sight. This is true, but as I had no assistant, it was not practicable. However, I was careful not to give the cats any cue to the correct response, by any difference of attitude when the food notes were sounded and when the other notes were played. So it does not seem possible to attribute the reactions of the animals to anything else than the association of a certain note with food-getting, and the consequent discrimination of that note from the other notes. Moreover, several observed incidents in the course of the experiments, such as getting up at the wrong note and *getting down at once*, strengthen this conclusion. Furthermore, the looks and actions of the animals, to an unbiassed observer, would indicate such clear discrimination of the notes. We conclude, therefore, that cats, or at least some cats, discriminate musical pitch, and also discriminate noises of different degrees of intensity.

It will be noted that in the experiment in which two individuals were tested, i.e., in the discrimination of a difference of two octaves of pitch on a harmonica, while the younger animal formed the association in 45 trials, the older animal required 90 trials to perfect the association. Again, as compared with the ability of raccoons, in similar tests, of the discrimination of the difference of two octaves of pitch on a harmonica, while the cats took respectively 45 and 90 trials, the two raccoons tested required 100 and 150 trials respectively to form the association. In exactly similar experiments which the writer made on two Rhesus monkeys, one individual formed the association in 30 trials, and the other in 40. Though, from the fewness of the individuals used in these different experiments, we are not warranted in drawing final conclusions as to the comparative rapidity of the formation of such associations in cats, raccoons and monkeys, the indications, however, point to the conclusion that Rhesus monkeys form such associations with somewhat more rapidity than cats, and with considerable more facility than do raccoons under similar experimental conditions.

NOTES

A NOTE ON THE SUPPOSED OLFACTORY HUNTING-RESPONSES OF THE DOG

H. M. JOHNSON

Nela Research Laboratory, National Lamp Works of General Electric Co., Nela Park, Cleveland Ohio.

Our present inability to measure or control olfactory stimuli may have some bearing on the fact that the dog's sense of smell has been avoided by careful experimental investigators. A number of problems in this field are highly interesting even though they do not lend themselves to treatment by quantitative methods. The supposed olfactory responses made by the dog in hunting are especially puzzling. At present the only available data are purely anecdotal, and these are meager, conflicting and untrustworthy.

Various assertions have been made as to the ability of the trained hunting-dog to trail his quarry. The belief is widespread that the bloodhound can follow a trail over 24 hours old without back-tracking. Let us accept provisionally a seemingly conservative statement; that a fox-hound can follow a three-hour-old trail of a rabbit without back-tracking, and assume that this is very near the limit of the dog's ability. A casual examination suffices to show the difficulty of explaining the dog's behavior.

Many hunters have said in effect that the dog follows the trail in the direction taken by the rabbit because the tracks made recently excite more intense smell-processes than do the older tracks. This explanation is not satisfactory. Suppose that in each of a series of tracks, *a*, *b*, *c*, etc., a like quantity of the same single smell-substance had been deposited by the rabbit; that the tracks had been made one second apart, and that *a* was made three hours ago. It is evident (*changes of chemical composition being excluded*) that the smell-substance is greatest in quantity when first deposited. It becomes dissipated in time so that in this case there is barely enough left in the track *a* to affect the dog.

If the smell-substance is deposited in a gaseous state, its diffusion could be represented by one of the well-known "curves of decay." The absolute intensity of the stimulus (i.e., the amount of odorous substance present in the track at a given moment of time) may, within limits, be formulized:

$$\text{Log } S_t = \text{Log } S_o - kt,$$

wherein S_o equals the amount of the substance first deposited, t the time which had elapsed since the deposit was made, and k a constant function dependent on conditions of temperature, pressure, etc.

In the case under consideration the stimulus-intensity at the track *a* is nearly zero when it is presented to the dog. The absolute difference of stimulus-intensity at *a*, *b* and *c* would have to be extremely small, since the difference in the respective values of t is of the order of one part in nearly 11,000. Further: even this difference between *a* and *b* would exist only if they were simultaneously presented. Since the dog is supposed to be following the trail of the rabbit, for him to be affected by even a part of the difference between *a* and *b* it is necessary that he travel faster than did the rabbit in making the tracks. If the dog travels at the same rate as did the rabbit, when he reaches *b* its intensity will be just equal to that of *a* when *a* was passed. Moreover, in actual practice other difficulties arise. Suppose the rabbit has run from moist ground to dry ground. The smell-substances are diffused more rapidly under conditions of relatively small humidity that under conditions of greater humidity. The stimulus-intensity of the recently made tracks on dry ground could thus be less than those made earlier on the wet ground. In such case our assumption fails to explain the dog's failure to show confusion.

But the dissipation of the smell-substance may be a complex process. For instance, it may be deposited, not in a gaseous state, but as a liquid or solid. In such case vaporization must precede diffusion. Vaporization, conditions being constant, proceeds at nearly a uniform rate in the open air. The amount of substance present in a gaseous state might thus be as great at a very advanced stage of dissipation as at an earlier stage. Since the substance to be odorous must be gaseous, we are not warranted in assuming that the stimulus-intensity is greater at a recently made track than at one made earlier, unless we know that all the smell-substance in the later track has been vaporized.

There may be other factors such as chemical changes by which the deposited substance becomes odorous, etc., but consideration of them only increases the presumption against the intensity-difference theory.

It has been suggested also that the dog may have an acute olfactory sensitivity to the *form* of the tracks made by his quarry and follow the trail from heel to toe. Certain features of the dog's behavior certainly indicate that he is *very* sensitive to differences of spatial position of olfactory stimuli. Another suggestion is that the smell-substances deposited by the different parts of the foot or body may differ specifically in stimulating quality, and that the dog is affected by this difference. Assuming either of these suggestions as a complete explanation of the dog's hunting behavior would require us to expect a bloodhound striking a man's trail at right angles, to back-track if the man had walked backward instead of forward across the field.

Dr. P. W. Cobb has suggested a simple hypothesis; that the dog's sense of direction may be due to the trailing of *ground* smell-substances. For instance: the smell-substances affecting a dog trailing a man who had crossed a mint-bed might be (1) ground + man; (2) ground + man + mint, the mint being intense; (3) ground + man + mint, the mint-smell-substances diminishing rapidly in the direction the man had taken. The hypothesis impresses the writer as being valuable, although it does not afford a complete explanation of the facts as variously alleged.

The value of careful field-tests should be apparent. The question may well be raised whether the hunting-behavior of the dog is really an olfactory response. A comparison of the field-behavior of anosmic dogs and normal dogs of the same litter and of a hunting breed, such as the beagle-hound, should prove highly interesting. It would be well worth while to ascertain as a beginning what responses a good hunting dog actually makes when introduced to trails the time and direction of which had previously been ascertained. The effect of numerous disturbing factors which could be introduced, some of which have been suggested above, ought to be quite interesting. It is to be hoped that some one with proper facilities and ample training may become interested enough to make an experimental investigation in this field.

JOURNAL OF ANIMAL BEHAVIOR

VOL. 4 MARCH-APRIL, 1914 No. 2

LIGHT DISCRIMINATION IN THE ENGLISH SPARROW

EUPHA FOLEY TUGMAN, A.M.
From the Psychological Laboratory of Indiana University

CONTENTS

PAGE
I. Introduction 79
  (1) Statement of the problem.
  (2) Previous experimental work.
  (3) History of the investigation.
    (a) Preliminary experiment.
II. Method 83
  (1) Care of the birds.
  (2) Method of handling the birds.
  (3) Description of the apparatus.
  (4) Experimental procedure.
  (5) Calibration of the lights.
III. Results 89
  (1) Threshold of discrimination.
    (a) Comparison with human threshold.
  (2) Method of learning.
    (a) Tables and results for each bird.
    (b) Comparison of results.
  (3) Incidental results.
    (a) Individuality.
    (b) Influence of former experiences.
    (c) Position habit.
    (d) Mental instability.
    (e) Relation of time to the failure or success of choice.
    (f) Effect of 48 hour interval between successive series.
    (g) Persistence of stimulation.
IV. Questions suggested by this investigation 107

I. INTRODUCTION

(1) *Statement of the problem.*—This investigation was pursued for the purpose of determining (1) the threshold of brightness discrimination in the house (English) sparrow, and (2) the behavior which the sparrow exhibits and the habits which it forms in learning to make such discrimination.

(2) *Previous experimental work.*—Considerable work has been done in experimenting on the learning methods and capacities of animals, from amoeba to man. Only recently, however, have investigators begun to study the delicacy and completeness of the sensory equipment of animals. Of most importance in connection with the present investigation is the work of Breed,[1] Cole,[2] and Bingham[3] on chicks, and Porter[4,5] on birds.

Breed[1] used the discrimination method in experimenting with chicks. His results show that his chicks could discriminate between black and white, different colors, and two objects of different size. He made form tests also, but his chicks gave negative results.

Cole[2] used the discrimination method in studying " the relation of strength of stimulus to the rate of learning in the chick." His results seem to indicate that when discrimination is easy the number of trials necessary for learning is less than when the discrimination is difficult.

Bingham[3] experimented on size and form perception. His chicks were punished by electric shocks when they made a wrong choice, and were rewarded with " food, light, warmth, and companionship " when they discriminated properly and were thus able to reach their nest box. He found that " the chicks' threshold of difference in size perception lies between one-fourth and one-sixth when the diameter of the standard circle is 6 cm." He holds that " earlier experimenters on the chick's perception of forms have failed to eliminate all possible conditions for discrimination other than the factor of form. * * * Reactions to optical stimuli which have been interpreted by observers as indicating form discrimination are probably made on the basis of unequal stimulation of different parts of the retina. * * *

---

[1] Breed, F. S. The Development of Certain Instincts and Habits in Chicks. *Behavior Mono.*, vol. 1, No. 1, Nov. 1, 1911.

[2] Cole, L. W. The Relation of Strength of Stimulus to Rate of Learning in Chicks. *Journal of Animal Behavior*, vol. 1, No. 1, 1911. Page 111.

[3] Bingham, H. C. Size and Form Perception in Gallus Domesticus. *Journal of Animal Behavior*, vol. 3, No. 2, 1913. Page 65.

[4] Porter, J. P. A Preliminary Study of the English Sparrow and Other Birds. *Amer. Jour. of Psych.*, vol. 13, 1904. Page 313.

[5] Porter, J. P. Further Study of the English Sparrow and Other Birds. *Amer. Jour. of Psych.*, vol. 17, 1906. Page 248.

A chick can acquire a perfect circle-triangle reaction, but control tests show that it has no general idea of circularity in contrast with triangularity."

Bingham's conclusion is that "the order of importance of factors in the chicks vision is size, brightness and general illumination, and form."

Porter's[6] work is more directly related to the present investigation since he experimented with English sparrows. He first studied their method of approaching food, and found that they alight some distance from the food and then hop to it. He then studied their rate of learning to open a latch on a food box and of finding their way through a maze. He found that the sparrows learned quite rapidly by the trial and error method. They exhibited some ability to profit by experience, also to some extent by imitation. Porter then tested the number sense of the English sparrow in the same way that Kinnaman[7] did with monkeys. The birds could not count, but showed some sense of position. When the food glass was covered with colored papers of the standard yellow, blue, red, and green, the birds were able to distinguish the colors. Various forms of food boxes were then used and the food was placed in one of them, the position of which was changed from time to time. This test was made on one bird only—a female. She was unable to distinguish the forms.

In his later work Porter[8] experimented with English sparrows, vesper sparrows, a cowbird, and a pigeon, attempting to compare the rates and methods of learning of the different birds. In learning the simple maze the vesper sparrow was the slowest. There was little difference between the others. All showed good memories, the cowbird being best. With the puzzle box the sparrow learned most rapidly. Porter then tested the birds for discrimination of three horizontal black lines on a card from a blank card; a card marked with a black diamond from a blank card; and two marked cards from each other. Both the English sparrow and the cowbird learned to distinguish these designs, but the sparrow showed some superiority in being able the more quickly to unlearn an old habit and to learn a new one. In discriminating colors all the birds did about equally well, except the sparrow which showed superiority in the case of blue.

---

[6] Porter, J. P. A Preliminary Study of the English Sparrow and Other Birds. *Amer. Jour. of Psych.*, vol. 13, 1904. Page 313.

[7] Kinnaman, A. J. Mental Life of Two Macacus Monkeys in Captivity. *Amer. Jour. of Psych.*, vol. 15, 1902.

[8] Porter, J. P. Further Study of the English Sparrow and Other Birds. *Amer. Jour. of Psych.*, vol. 17, 1906. Page 248.

(3) *History of the investigation.*—(a) Preliminary experiment. This investigation was begun in the Psychological Laboratory of Indiana University on February 8, 1911. Twenty-six house sparrows were obtained but seventeen soon died. The experiment was begun with the nine remaining birds. Two birds were tested to see if they could be trained to choose the darker of the two stimulus areas. One was given 38 trials but chose the darker side only six times or 14% of the time. The other bird was given 32 trials and it chose the darker side 5 times, which is 14%. Then both birds died. The other seven birds were allowed to choose the brighter side which seemed to be the natural tendency. But the experiment was not continued very long as these birds also died. However, the few results obtained seemed to show that all the birds were able to discriminate the wide differences in intensities used.

The preliminary experiment was important in that it showed wherein the apparatus and method needed revision. One of the most important changes made in the apparatus was in the method of producing a motive. In the preliminary experiment the floor of the discrimination chamber was covered with parallel copper wires one centimeter apart. The wires were connected so as to form an interrupted circuit in connection with the induction coil and key. This was the plan used by Yerkes[9] in his experiments with the dancing mouse. But the sparrows rested with their feet in a sort of arched position with only the claws touching the wires. Consequently it was not easy to shock them. It was necessary to construct perches as described in a later section of this paper, and as used in the final experiment.

In October, 1911 the writer resumed the experiment with four birds,—two males and two females. The work continued until June, 1912.

---

[9] Yerkes, R. M., 1907. The Dancing Mouse. The Macmillan Co., N. Y.

II. METHOD

(1) *Care of the birds.*—The writer found it very difficult to keep sparrows alive in captivity. The birds were kept in a large cage before a large, open window in the experiment room. They were provided with an abundance of Spratt's mixed bird seed, fish bone, and clean water. The adjustable floors of the cage were cleaned frequently and covered with coarse sand. But for some unknown reason many sparrows died, usually in spasms. The experimenter found that the best plan was to cage the sparrows some weeks before beginning an experiment. If they died it was usually very soon after being placed in confinement. If they survived the first few weeks it was reasonably safe to begin an experiment with them. The four birds used in the final experiment kept in good physical condition until near the end of the investigation. One died in spasms shortly before the end of the experiment, and two others shortly after. The cause of death was not apparent. The fourth bird is still alive, after a confinement of one and a half years.

(2) *Method of handling the birds.*—In the preliminary experiments the writer tried handling the birds. This seemed to make them wilder, instead of taming them. To avoid the necessity of handling the birds the writer constructed a box 24 x 19.5 x 15 cm., and covered it with wire mesh. It was provided with a handle, and with a door at the end, and was used to transfer the birds from the cage to the apparatus. Against the back wall of each half of the cage was an inside adjustable wall of wire which, when pulled forward, forced the bird out at the door at the front, and into the portable box. Then the door of the box was closed and the bird carried about at will by the experimenter. This seemed to be a very good method of handling the birds as it did not frighten them after the first few times.

(3) *Description of the apparatus.*—The apparatus used in the investigation consisted of the Yerkes-Watson brightness apparatus,[10] and an experiment box modelled after the one described by these authors.[11]

---

[10] Robert M. Yerkes and John B. Watson. Methods of Studying Vision in Animals, pp. 17–24.

[11] Ibid, pp. 24–25.

The discrimination box is shown in Fig. 1 as that portion of the apparatus below the line EE^1 and marked DB. It is built of wood and blackened inside and out with several coats of lamp black and oil so as to make it a dull black. Very little light is reflected from the sides of the box. The box consists of an entrance chamber (C, Fig. 1) which is 5 x 4.5 x 19.5 cm.; the discrimination chamber is 54.5 x 46 x 19.5 cm., and is divided at the end next the light box by a partition 30 cm. long, into two identical compartments, C_1 and C_4. Alleyways, C_2 and C_3, which are 86 x 8 x 10 cm. connect C_1 and C_4 respectively with the compartments C_3 and C_6, both of which open into the entrance chamber C. These various compartments are separated by sliding doors D_1, D_2, D_3, D_4, D_5, D_6 and D_7, operated by

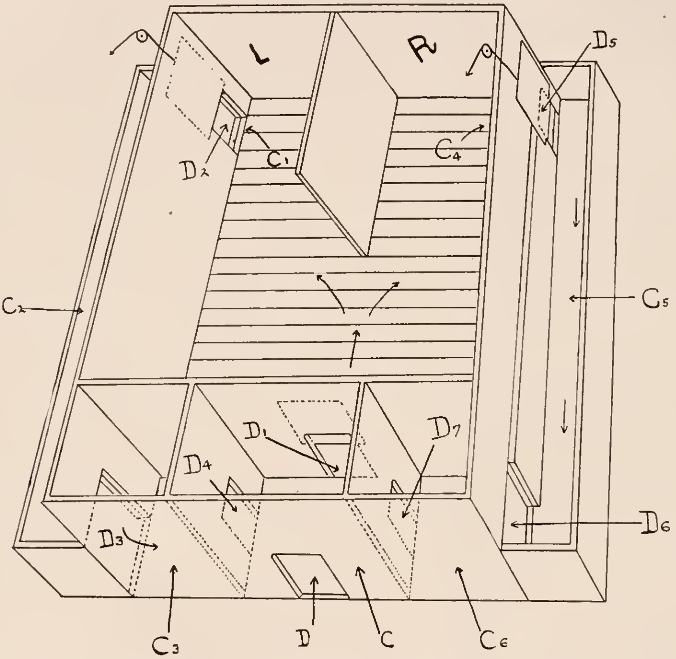


FIGURE 1. Discrimination Box. Openings indicated by D, chambers and alleys by C. Route of bird could be either C, D_1, C_1, D_2, C_2, D_3, C_3, D_4, C, or C, D_1, C_4, D_5, C_5, D_6, C_6, D_7, C. Discrimination made after passing through D. Cross lines in discrimination chamber indicate perches 2cm. above floor. Split brass tubes, stuck on wooden core with paraffine, form broken circuit which could be closed by bird grasping perch in alighting.

means of a system of cords and pulleys leading to the front end of the apparatus.

Two centimeters above the floor of the large discrimination chamber and four centimeters apart are perches across the box. The perches were made of three-eighth inch 22 gage brass tubing, oxidized and slit longitudinally into two halves. The two halves of this tubing were placed on either side of a .5 inch wooden core and held in place with paraffine. One-half of each perch is connected to one terminal and the other half to the other terminal of a Williams' Dial induction coil whose primary is in circuit with two dry batteries. A hand key is placed in the circuit and the secondary coil shifted to a position so that when a bird is resting on a perch it may be shocked by closing the circuit at the key. It is natural for the bird to hop from one perch to another and grip the perch with the feet. So when the feet are moist they can be shocked very effectively. A wet pad is kept in the entrance chamber C (Fig. 1) to keep the bird's feet moist. When dry the horny epidermis serves to protect them from the electric discharge.

The whole discrimination box is covered with .5-inch wire cloth, not shown in Fig. 1. The chamber C, and the near portion of C_1 and C_4 are covered with black velvet paper which prevents the bird from seeing the experimenter and the experimenter from seeing the bird until after the bird has discriminated and hopped to either C_1 or C_4.

(4) *Experimental procedure.*—Before beginning the experiments each bird was left in the discrimination box for twenty-four hours. All the doors were left open so that the bird could thoroughly acquaint itself with the apparatus. The use of artificial light for illuminating the stimulus areas made it necessary to conduct all the tests in a dark room. The birds were kept in the dark room so that they would not be excited by being moved from one room to another and also would become accustomed to the darkness and to the noise of the induction coil.

A small electric light in the room was turned off during each single test and then turned on again as soon as the bird had made its choice of the stimulus area and passed on into the alley.

On succeeding days (Sundays excepted) each bird was given a series of 15 trials. A trial consisted in requiring the bird to discriminate between the two stimulus areas in order to return to the nest box without receiving a shock. Two of the birds, Male V and Female VI, were required to choose the darker area and the other two birds, Male IV and Female V, were required to choose the brighter area. The two groups of birds were otherwise experimented upon in identically the same manner. Throughout the whole investigation the same order in shifting the lights was given to all four birds. The standard light was shifted to one side or the other at frequent and irregular intervals. The order was such that the standard light was on the left side the same number of times as on the right side.

Table I gives the relative position of the standard light during the first 225 trials. The other positions were similar to the ones shown in Table I. When the standard intensity (.098 c.p.) was in the position L (Fig. 1) the letter L was used. That means the standard was on the left. When the standard was on the right (at R, Fig. 1), the letter R was used. Since two birds were trained to go to the darker side L means for them that the darker light was on the left side and the brighter on the right. In the positions marked R the darker light was on the right and the brighter on the left.

TABLE I

Position of Standard Light for the First 225 Tests

Series	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Preference	L	R	R	R	R	L	L	R	L	L	..	..	..	..	..
1	R	R	L	L	R	L	R	R	L	R	R	L	R	L	R
2	L	L	R	L	R	L	L	R	R	R	L	L	R	L	L
3	L	R	L	L	L	R	R	L	R	R	L	R	L	L	R
4	L	R	R	L	R	R	L	L	R	R	L	R	L	R	L
5	L	R	L	L	R	R	L	R	L	R	R	R	L	R	L
6	L	L	R	L	R	R	L	L	R	R	R	L	R	L	L
7	L	L	R	L	L	R	L	R	R	L	L	R	R	L	R
8	L	R	R	L	R	R	L	R	L	R	L	R	L	R	L
9	L	R	L	R	R	L	R	L	L	R	R	L	R	L	L
10	R	R	L	R	L	R	L	L	R	L	R	L	R	R	L
11	R	L	R	L	L	R	L	R	L	R	L	L	R	R	L
12	R	R	L	L	R	L	R	L	R	R	L	L	R	L	R
13	L	R	L	R	L	L	R	R	L	R	L	L	L	R	R
14	L	R	R	L	L	R	L	R	R	L	R	L	R	L	R
15	R	L	R	L	L	R	L	R	L	L	R	R	L	R	L

The sources of light used were two 25 watt, 110 volt Mazda lamps, which were as near alike in quality of light as the experimenter was able to judge. The apertures in the stimulus adapter were 6 cm. in diameter.

The lamps were occasionally interchanged to prevent the birds from forming any habits due to difference in the quality of the light which the observer was unable to detect. The discrimination box was frequently washed out as a precaution against the bird getting any "cues" or reflections due to the waste material which collected.

The procedure for each test was as follows: The bird was placed in the entrance chamber (C, Fig. 1) on the wet pad. The light in the room was then turned off and the induction coil started. After waiting several seconds to accustom the experimenter's eyes to the darkness, the door D_1 was opened and the bird allowed to pass into the discrimination box. (The entrance chamber was covered with black velvet paper and consequently was always dark. Hence the bird's eyes were accustomed to the dark.) Having entered it the bird could return to the entrance chamber only by passing through to the right or to the left of the partition and then through either door D_2 or D_5 and thence to C by way of the narrow alleys C_2 or C_5 through C_3 or C_6 and through doors D_4 or D_7 into the entrance chamber. After passing through the door D_1 the bird nearly always hesitated several seconds and frequently several minutes, before making a choice between going to one or the other of the stimulus areas. If the bird chose correctly it was allowed to pass on into the alleyway and back into the entrance chamber. But if it made a wrong choice the circuit was closed at the key and the bird shocked. The birds learned very soon that when they received an electric shock they must go back and around the partitions to the other side. In the earlier experiments the birds would often stop just beyond the door D_1. In such cases the experimenter gave them instantaneous shocks which caused them to move on and thus force them to discrimnate. But after they learned what they were expected to do and discrimination became established, they would hesitate only a few seconds before making a choice. In the later experiments it was seldom necessary to shock them except when they made a wrong choice.

A series of correct choices for two consecutive days—30 trials—was counted as correct discrimination and the difference in intensity of the standard and the variable light was decreased. At the beginning of the investigation the standard light was placed at 38 cm. from the stimulus area, thereby giving it a measured intensity of .098 c.p. The variable light was placed at 238 cm. from the stimulus area, thereby giving it an intensity of .0025 cp.. After two consecutive days of correct choices the variable light was moved closer to the standard, which was always in the same position. Thus the intensity of the variable was increased each time, and the difference between the standard and the variable decreased in the same ratio. Each shift in the variable light necessitated the bird learning the problem again. It usually required a shorter time than the original problem, yet each shift was really a new problem to the bird. The difference between the standard and variable was decreased step by step until the bird was unable to discriminate between the two areas. Then the difference between the standard and the variable was increased step by step until the bird was able to discriminate between the two areas. The threshold of discrimination was taken as the difference between the least discriminable difference in the descending series and the least discriminable difference in the ascending series.

Full records were kept during the progress of each series, showing the relative positions of the standard light at each trial, the time consumed in making each choice, the success or failure of the trial, and full data regarding the actions of each bird during each trial. The characteristics of the individual birds, methods of learning, etc., and the tables and results are taken from these records.

(5) *Calibration of the lights.*—The light sources and the stimulus areas were calibrated near the beginning of and frequently during the investigation with a Lummer-Brodhun photometer against a Tungsten light, standardized at 1 c.p. in Hefner units.

The photometer readings were first taken with the light sources 38 cm.[12] back of the ground glass stimulus area. After the intensity of the stimulus area was calculated with the light source at this position, the intensities of the stimulus areas were calculated for the other positions of the light source.

The intensities shown in Table II are calculated from the readings taken on June 1, 1912, which was during the time that the birds were making the most difficult discrimination.

---

[12] The first experiments were made before this reading was taken. It was unfortunate that the light was not set nearer the glass and thus have given a reading of 1.c.p. instead of the decimal .098.

TABLE II

The figures in the first column indicate the number of discriminations required. The second column shows the c. p. of the standard light, calculated in Hefner units which remained the same throughout the experiment. The third column indicates the c. p. of the variable light and the last column shows the difference in intensity between the standard and variable.

Position	Intensity of Standard	Intensity of Variable	Discriminated Difference
1	.098	.002	.096
2	.098	.003	.095
3	.098	.004	.094
4	.098	.006	.092
5	.098	.008	.090
6	.098	.010	.088
7	.098	.015	.083
8	.098	.019	.079
9	.098	.024	.074
10	.098	.043	.055
11	.098	.046	.052
12	.098	.048	.050
13	.098	.062	.036
14	.098	.065	.033
15	.098	.068	.030
16	.098	.073	.025
17	.098	.076	.022
18	.098	.081	.017
19	.098	.085	.013
20	.098	.089	.009

III. RESULTS

(1) *Threshold for discrimination.*—Table III shows the four sparrows' threshold of discrimination for the standard intensity .098. The second column gives the least difference between the intensities of the standard and the variable illuminated areas

TABLE III

Showing the threshold of brightness discrimination for each of the four birds.

Bird	Least Discriminable Difference, Descending Order	Least Discriminable Difference, Ascending Order	Estimated Threshold
Male IV.......	.013	.017	.015
Female V......	.036	.033	.035
Male V........	Discriminating at .03 when he died	....	....
Female VI.....	.022	.022	.022

which each sparrow was able to discriminate in the descending series. The third column gives the least difference which each sparrow was able to discriminate in the ascending order. The last column gives the average of these two which is taken as the threshold of discrimination for the standard .098 c.p.

(a) Comparison with human threshold. The experimenter, using the same apparatus and methods, investigated light discrimination in three human subjects in order to compare the results with those obtained with the birds. Two of the human subjects were required to choose the darker and one the brighter of the two stimulus areas. The subjects are spoken of as A, B, and C. B gave very much better results all through the investigation than did either of the others and he responded to the darker of the two lights. C did not give very good results. He responded to the darker of the two lights. C was partially color blind and yet he was always seeing yellow or red in the lights. He said that the color in the lights confused him. This fact may have caused his poor results. The experiment with the human subjects was interrupted many times and often several days would elapse between successive series. This undoubtedly had some effect on the judgments. As the observers' time was limited, the work was not done as thoroughly or as completely as in the case of the birds. The thresholds are not absolute but are estimated from the limited data at hand. Table IV gives the estimated thresholds for both the birds and the

TABLE IV

Comparison of brightness threshold for the four sparrows and the three human subjects.

Group	Subject	Estimated Threshold of Discrimination for the Standard Intensity=.098 c.p.
Bird	Male IV	.015 c.p.
	Female V	.035 "
	Male V	.03 (died)
	Female VI	.022 c.p.
Man	A	.013 c.p.
	B	.009 "
	C	.013 "

human subjects. There seems to be little doubt that for the particular intensity the human subjects have a very much smaller threshold of discrimination than do the birds. However, Male IV could discriminate almost as fine a difference in intensity as did two of the men. When the difference between the two lights became very small two of the subjects found that they were simply guessing and not really discriminating. Yet their results appear very good. So even from the results it is very difficult to determine just what their thresholds of discrimination are.

(2) *Methods of learning.*—The data which this investigation gives regarding the learning process of sparrows is fully as important as the light which it throws on the threshold of visual discrimination. More problems were of course raised than were answered, but much light is thrown upon many of the factors which condition animal learning and which in turn condition the sensory threshold which an animal may acquire. One of the most striking facts is the very large number of trials necessary to bring the animal to the threshold. The three animals for which the threshold was determined averaged 2420 trials each. For the discrimination of the lowest threshold they averaged 480 trials each; one of them discriminating only after 615 trials. This bird was trained daily, Sunday excepted, from April 8th until May 31 before she made a record of perfect choices for two days in succession.

(a) Tables and results for each bird. The results for each bird were tabulated in a regular form which stated the intensity (in Hefner units) of both the standard and the variable lights for each separate position; the difference between the intensity of the standard and the intensity of the variable; the date of each series; the number of each series; the number of right choices; the number of wrong choices; the number of times the wrong choices occurred when the standard was on the left; the number of times the wrong choices occurred when the standard was on the right; and the percentage of error for each series.

Male IV was allowed to choose the brighter of the two illuminated areas. The intensity of the standard was .098 c.p. and at the beginning of the experiment the intensity of the variable was .002 c.p. After each successful series of 30 choices the light was shifted.

On November 21st the difference in intensity between the standard and the variable lights was shifted from .036 c.p. to .022 c.p. This seemed to be too large a step and confused the bird, so on November 28th the difference was placed back at .036 c.p. and the bird soon relearned that discrimination. Then when the difference in intensities was reduced in smaller steps the bird learned to discriminate the lights with differences much smaller than .022. In the descending series the least discriminable difference in intensity was .013 c.p. When the intensity was reduced to .009 c.p. the bird seemed wholly incapable of discrimination and very soon fell into the position habit. When the intensity was increased to .013 c.p. the experimenter was unable to break up the bird's position habit though it had discriminated the lights at this position in the descending series. Finally the lights were moved still farther back to .017 and after 14 days the experimenter succeeded in breaking up the position habit. The bird was again able to discriminate the illuminated areas. Hence the position midway between .013 and .017 c.p. is taken as the least discriminable difference. That position gives the difference in intensity between the standard and the variable as .015 c.p. Of the 599 wrong choices the bird made 223 when the brighter light was on the right and 376 when it was on the left.

Female V did not give as good results. This the observer attributed to the fact that she was always so frightened that she would never hesitate long enough to make a discrimination. She apparently had little position habit but simply went to one side or the other in a confused manner. She made the necessary 30 consecutive correct choices with the difference in intensity .036 c.p. But when the position was shifted giving a difference in intensity of .030 c.p. she was not able to discriminate even after 540 trials. So the variable light was moved back, increasing the difference to .036 c.p. and after 600 trials she finally made 30 correct choices. Hence the least discriminable difference for Female V is .033 c.p.

Out of 434 wrong choices 305 were made when the brighter light was on the right and 129 when the brighter light was on the left.

For Male V and Female VI the problem was very much more difficult. They had to overcome their natural tendency to go always to the brighter light, and learn to choose the darker light. It took Male V 165 trials and Female VI 270 trials to learn the problem. Table V shows the record made by the two sparrows in learning the problem. The first column gives the number of each series of 15 trials. The second and fifth columns give the average percentage of error (series divided into small groups) for Male V and Female VI respectively. The averages show a decided decrease in the percentages of error made by the birds during the learning of the problems. The third and sixth columns show the percentage of error for the daily series of 15 trials each, for each of the birds. The fourth and last columns give respectively the average percentage of error for the first

TABLE V

Showing errors made in learning the first discrimination by the two birds which were trained to choose the darker light. The middle column in each group shows the percentage of errors made in each test. In the column to the left of the middle, the period of learning is divided into thirds and the average percentage of error is calculated for each third. In the column to the right is given the percentage of error for each half of the learning period. Despite occasional lapses as shown by increased percentage of error for single days, each of the later groups of days shows a decided lowering of the error percentage. This shows the gradual aspect of the learning process.

	MALE V			FEMALE VI		
Number of Series	Average per cent of Error	Percentage of Error Daily Series	Average per cent of Error	Average per cent of Error	Percentage of Error Daily Series	Average per cent of Error
1	45	60	42.1	50.6	42	44.8
2		40			42	
3		40			60	
4		40			40	
5	38.7	40			60	
6		33			60	
7		42	15.4	33.	40	
8		40			40	
9	5.2	0			20	
10		13			66	19.6
11		13			6	
12		0			26	
13		0		16.5	20	
14					13	
15					26	
16					20	
17					0	
18					0	

half and the last half of the trials required to learn the problem. The figures also show a decided decrease in the percentages of error as the birds gradually learn the problem.

The curve (Fig. 2) is plotted from these results. The ordinates indicate the percentage of error and the abscissa, the number of the series—each series consisting of 15 consecutive trials. The solid line (———) is the error curve for Female VI and the broken line (- - - - -) for Male V, while learning to go to the darker side. The table and curve show that the sparrows varied in their daily record as well as in the time required to learn completely the problem. The table shows also that the birds exhibited great instability even until the end of the experiment. Male V made one wholly perfect series of 15 trials—the ninth series. Female VI did not make a perfect daily record until the 30 correct choices were made in succession.

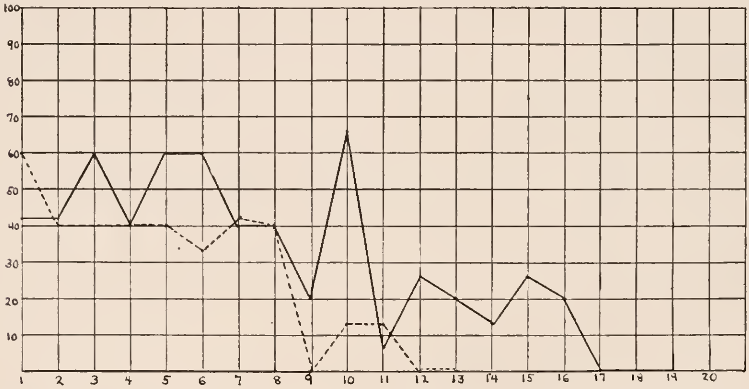


FIGURE 2. Curves showing percentage of errors made by two birds, Male V (- - - - -) and Female VI (———) while learning to choose the darker of two illuminated areas. Despite occasional lapses the learning appears to be a gradual process.

The progress of Male V toward the threshold was very slow. The observer felt that the bird really could discriminate the lights long before it gave perfect tests. But it was more hasty in making a choice than Female VI, with less attention and effort at discrimination. When Male V died he had been given 1515 tests and was working with the difference in intensities at .03 c.p. When Female VI had been given 1515 tests she was working with the lights at the discriminable difference .017 c.p.

Female VI had reached a point much nearer the threshold than had Male V after the same number of trials. Male V made 295 wrong choices, 184 when the brighter light was on the right and 111 when it was on the left. The observer had expected Male V to give better results than any of the other birds because he was in the same cage with the other birds and in the same room where the experiments were conducted for two months and a half before he was experimented upon. He did learn the problem more quickly than Female VI, but then fell behind her after the first change in the intensity of the lights. Male V died before the experiments were finished so his threshold of discrimination was not reached.

Female VI was a very satisfactory bird with which to work. After she once learned to choose the darker of the two illuminated areas, she would always stop just a few seconds outside the door (D_1, Fig. 1), look to one side and the other and then hop on calmly to the light she had chosen. She was never excited but always slow in her movements. She worked gradually toward the threshold. When the variable light reached 43 cm. with the standard at 38 giving a difference of intensity of .022 c.p. she discriminated immediately. The variable light was moved to 42 cm. thus giving a difference in intensities of .017 c.p. At this position she was given 720 trials, with 24 the percentage of error. But she apparently could not discriminate well enough to give two days of perfect trials. So the variable light was shifted back to 43 cm., giving a difference in the intensities of the lights of .022 c.p. At this point it took 450 trials before she gave 30 perfect trials in succession, while in the descending series she gave 30 perfect trials after having made only one wrong choice out of the 30 preceding trials. She had evidently been so puzzled with the lights when the difference in intensity was only .017 c.p. that she had either forgotten the problem or had formed the habit of not trying to discriminate. Whatever the cause it took her 450 trials to learn the problem which she had learned in the descending series in 30 trials. Out of a total of 414 wrong choices 262 were made when the darker light was on the right and 152 when it was on the left.

Hence the least discriminable difference for Female VI was .022 c.p., a difference of 5 cm. between the position of the standard and the variable light.

(b) Comparison of results. Table VI shows a summary of the results for each bird. The first column gives the difference in intensity (c.p. Hefner units) between the standard and the variable lights in the decreasing series. The third column gives the number of trials it took each bird to learn to discriminate the lights at each position. The fourth column gives the number of correct choices and the sixth column gives the number of incorrect choices. The last gives the percentage of error of each bird for each intensity.

TABLE VI

Summary of results for each bird. Male IV and Female V chose brighter light Male V and Female VI chose darker light. Male V began discrimination with lights nearer together than did the other birds.

Difference in Intensity (Hefner Units) between the Standard and the Variable Light	Bird	Number of Trials	Right Choices	Wrong Choices	Per cent of Error
.096	Male IV Female V	30 30	30 30	0 0	0 0
.095	Female VI	240	150	90	37
.094	Male IV Female V Female VI	30 45 15	30 42 13	0 3 2	0 6 13
.092	Male V Female V Female VI	75 90 30	70 84 30	5 6 0	15 6 0
.090	Male IV Female V Female VI	30 30 15	30 25 14	0 5 1	0 16 6
.088	Male IV Female V Female VI	30 30 75	30 30 65	0 0 10	0 0 13
.083	Male IV Female V Male V Female VI	30 30 165 15	30 30 113 14	0 0 52 1	0 0 31 6
.079	Male V	30	30	0	0
.074	Male IV Female V Male V Female VI	30 15 30 30	28 10 30 30	2 5 0 0	6 33 0 0

TABLE VI—*Continued*

Difference in Intensity (Hefner Units), between the Standard and the Variable Light	Bird	Number of Trials	Right Choices	Wrong Choices	Per Cent of Error
.055	Male IV	30	30	0	0
	Female IV	135	85	50	37
	Male V	420	329	91	21
	Female VI	30	23	7	23
.052	Male V	210	146	64	31
.050	Male V	180	151	29	16
.036	Male IV	90	66	24	27
	Female V	45	41	4	8
	Male V	120	86	34	28
	Female VI	15	14	1	6
.030	Male IV	30	0	0	0
	Female V	540	415	125	23
	Female VI	285	229	56	20
Back at .033	Female V	600	496	104	17
.025	Male IV	15	14	1	6
	Female VI	30	0	0	0
.022	Male IV	90	66	24	27
	Female VI	30	29	1	3
.017	Male IV	225	181	44	19
	Female VI	720	557	163	22
Back at .022	Female VI	450	....	....	....
.013	Male IV	315	239	76	24
.009	Male IV	390	341	49	12
Back at .013	Male IV	360	306	54	15
Back at .017	Male IV	240	165	75	31

The following figures are made from this table. Figures 3 and 4 show the number of trials each bird required to learn to discriminate the light at the given intensity. The abscissae indicate the differences of intensity produced by the standard light and the various positions of the variable light. The ordinates indicate the number of trials required to learn the discrimination. Figure 3 gives the results for Male IV and Female V, both of which were allowed to choose the brighter of the two stimulus areas. The solid line (———) is the curve for Male IV and the dashed line (- - - - -) is the curve for Female V.

Figure 4 gives the results for Male V and Female VI. The solid line (———) represents the results for Male V. The abrupt ending is due to the bird dying at this point in the investigation. The dashed line (- - - - -) represents the results for Female VI. Both Male V and Female VI, as stated before, were trained to choose the darker of the two illuminated areas. The curves for Male IV and Female V (Figure 3) are not widely different until the threshold was reached for Female V. They begin practically the same. Both birds had little trouble in discriminating the areas when there was a wide difference in the intensities. When the difference in intensity was .055 c.p. Female V required 135 trials while Male IV made 30 perfect choices without any trouble. Then at the difference in intensity of .036 c.p. Female V made a better record than Male IV. But when the variable light was again shifted and the difference in intensity reduced to .030 c.p. Female V seemed wholly incapable of discriminating even after 540 trials. The difference in intensity was increased to .033 c.p. and after 600 trials she discriminated. For the descending series Female V had discrimi-

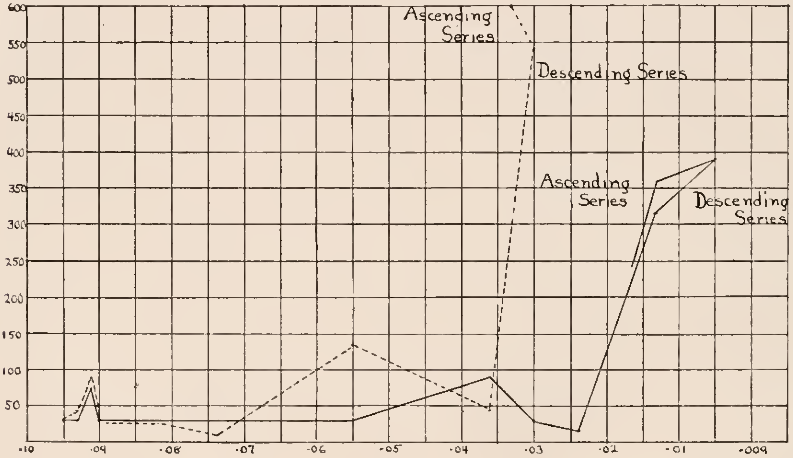


FIGURE 3. Number of trials necessary for Male IV (———) and Female V (- - - - -) to learn each discrimination. The difference in intensity is shown on abscissae. Number of trials is represented on ordinates. Both curves show large number of trials necessary when difference in intensity is small.

nated this same intensity after 135 trials. But when she failed with the difference in intensity .030 c.p. she seemed to have gotten into the habit of immediately going to one side or the other without any effort at discrimination. Consequently when the difference in intensity was later increased it took a long time to break up this habit. Male IV continued to discriminate the lights without hesitation until the difference in intensity was decreased to .025 c.p. Then the curve starts up abruptly. This shows that as the discrimination became more difficult, the bird required more trials to learn the discrimination. But when the difference in intensity of the illuminated areas was reduced to .009 c.p. Male IV was unable to learn the discrimination even after 390 trials. The difference in intensity was increased to .013 c.p. At this position he finally succeeded in learning the discrimination after 315 trials. But in the ascending series he was not able to learn to discriminate correctly even after 360 trials. The difference in intensity was increased to .017 c.p.

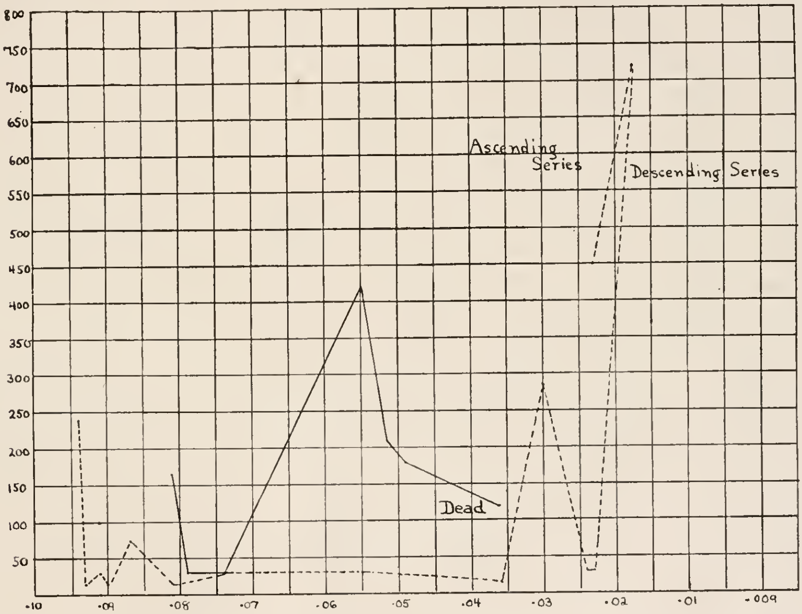


FIGURE 4. Number of trials necessary for Male V (———) and Female VI (- - - - -) to learn each discrimination. The difference in intensity is shown on abscissae. Number of trials is represented on ordinates. Curve for Female VI shows large number of trials necessary when difference in intensity is small.

and after 240 trials he succeeded in giving 30 correct choices. The observer felt that the bird could discriminate the areas when the difference in intensity was .013 c.p. But when he was on the .009 intensity he acquired the position habit which lasted through the 306 trials at the next position and almost until the end of the investigation.

Figure 4 represents the results of Male V and Female VI. The curves are more irregular than those for Male IV and Female V. The curve of Female VI is more nearly like those of Male IV and Female V than is the curve of Male V. The sudden drop in both curves indicates the fact that both birds learned to choose the darker of the two illuminated areas. After Female VI learned the first discrimination she had no trouble until the difference in intensity became small. She readily discriminated a difference in intensity of .022 c.p., but when the difference was reduced to .017 c.p. she was incapable of discriminating the areas even after 720 trials. The difference in intensity was then increased to .022 c.p. and after 450 trials she succeeded in discriminating the lights.

Male V learned to go to the darker of the two illuminated areas more quickly than did Female VI, but his other results were never so good as those of Female VI. The observer felt that the discrimination was really not difficult for the bird but that many of his wrong choices were due to fright. He often did not even attempt to discriminate the lights. He would go to one light and if he failed, would hurry around to the other side and into the alley way. He was beginning to give better results when he died.

(3) *Incidental results.*—The author has included under this heading some of the most interesting facts brought to light during the experiment with the birds.

(a) Individuality. As shown in the previous discussion, the sparrows exhibited distinct individual differences in their rate of learning. This was also true of their general behavior and of their method of attacking the problem. The individual birds also varied their course of procedure at intervals during the experiment.

All the birds were quick in learning the apparatus and its various alleyways. When they chose the wrong light and were shocked they very soon learned to turn and go around to the other light. They were slower to learn to enter the alleyways because they were dark and the bird avoids dark places. But even this natural tendency was overcome in a surprisingly short time.

The directness or indirectness of approach and entrance into the discrimination box varied in the different cases. Two of the birds would hesitate several seconds or even minutes before entering the discrimination box. But the other two seemed eager to go through the experiment. Male IV was calm and deliberate in his movements. He would hop into the doorway (D_1, Fig. 1) as soon as it was opened. He would sit in the doorway or just outside for several seconds, turning his head quickly to one side or the other. (All the birds looked at the lights with their heads turned to one side or the other. They never seemed to look at the lights with both eyes at the same time.) Then he would hop calmly on, to whichever light he had chosen. He never seemed excited and seldom required shocking. When shocked it required a heavy discharge to produce any effect.

Male V was always very much excited. For a long time he would dart out to one side or the other without attempting to discriminate the lights. Suddenly he changed his method and would hesitate a long time just beyond the door (D, Fig. 1). There he would sit, often for several minutes. Sometimes the observer would have to shock him before he would move. But usually after a long hesitation he would dart on to one light or the other. The observer felt that as a usual thing he did not rely upon visual discrimination. His judgments were never very satisfactory.

At the beginning of the experiment Female V would always hesitate in the doorway, discriminate between the lights and hop on. But later she acquired the habit of darting out to one light or the other the very instant the door was opened. For a long time it seemed absolutely impossible to break up this habit. Frequently there would be days when the bird seemed to show some improvement but in general she gave very poor results. Finally the observer decided that she did not have such good sight as the other birds and that she had really reached her threshold of discrimination. The difference in the intensity of the lights was increased a little and after a short time the bird began to discriminate them again. The previous behavior was evidently due to inability to make the discrimination.

Female VI was more calm than any of the other birds. Her behavior was even more satisfactory than the behavior of Male IV. After Female VI learned the first problem, to choose the darker of the two lights, she would move about very slowly and deliberately. She would hesitate in the doorway of the entrance chamber for a few seconds, then hop out into the discrimination box. She would hesitate several seconds looking a while to one side, then turning her head and looking to the other side. Presently she would hop on to the side she had chosen and into the alleyway. She was always slow making a choice and gave good results all through the experiment.

The nervous birds gave the poorer results.

Cole[13] thought the chicks which were most sensitive to the electric shock learned more rapidly under the influence of weak stimuli. The most sensitive sparrows did not learn most quickly. The two birds which gave the best results, Male IV and Female VI, both required a heavier shock than the other two birds. It was not necessary to shock them frequently. But when it was necessary, the observer had to give them almost twice the strength of current that was given the other birds. As stated before, the final results differed widely. Male V and Female V failed to discriminate lights with which the other birds had no difficulty. The observer thinks that Male V and Female V were inferior to the other two birds in acuteness of vision and probably in mental capacity also.

(b) Influence of former experiences. At first the birds were greatly influenced by their former experiences. They would tend to respond in the same direction as in the immediately previous test, provided they had not received a shock. If they had just received a shock they would nearly always go to the other light in the following test. But after the birds learned the problem their judgments were founded on visual discrimination and they were not guided much by previous experience except when they acquired the position habit.

(c) Position habit. The thing that gave the experimenter the most trouble was the tendency of the birds to get the position habit. The habit might appear at any time and the observer always had to be alert lest the habit get firmly fixed. If it did become fixed it was very difficult to break. It is evident the sparrow forms the habit of choosing by position much more easily than the habit of choosing by visual discrimination. The form of position habit which appeared most frequently was that of alternating from one side to the other without regard to the illumination. But the observer found that the birds learned also to go twice to one side, then twice to the other side, etc. A few times when the order required three choices in succession to one side, the birds would invariably want to go three times to the other side. The experimenter planned to try more complicated orders and see if the birds could be trained to learn the habit. Lack of time prevented her carrying out this part of the investigation.

---

[13] Cole, L. W. The Relation of Strength of Stimulus to Rate of Learning in Chicks. Journal of Animal Behavior, Vol. 1, No. 1, 1911. Page 111.

(d) Mental instability. The sparrows exhibited three quite distinct types of mental instability; all of which were sources of considerable trouble to the observer. At times the birds would go to one side or the other apparently without trying to discriminate. This is the first type. The second type of mental instability was the persistence in going to one side. When they would persist in this the experimenter found it quite impossible to do anything with them. The third type might be termed stubbornness or stupidity. When they would get stubborn or stupid they would simply refuse to move. They would pay no attention to an electric shock. The observer would force them around through the apparatus though the results obtained on such days were useless.

The experimenter noticed that all the birds seemed to have these periods of mental instability though they did not all have them at the same time. One day a bird would record an almost perfect series and the very next day a series of failures. It was noticeable that such stupidity nearly always succeeded a period of unusually good work on the part of the bird. The bird usually recovered from this stupidity as quickly as it had come on. Then the bird would continue the usual method of procedure as though nothing unusual had happened. A few times they recovered during a day's series and the last few results would be very satisfactory, while the first of the series were failures. The question which came to the mind of the experimenter was whether or not these periods of stupidity or stubbornness come at regular intervals. But she was unable to decide from the data at hand.

(e) Relation of time to failure or success of judgment. The human subjects thought that the hasty judgments were more often correct than the deliberate ones. The observer, as stated before, kept account of the time required to make each choice. Then she averaged about 500 of these times for each bird. The 500 times were taken as representative of the total data. They include the time required to make the choice for each of a day's series selected at intervals throughout the whole experiment. These times were averaged—the time of the correct choices in one column and the time of incorrect choices in another column. The results are shown in Table VII.

TABLE VII

Relation of time of choice to failure and success of judgment. Average of 500 choices taken at random throughout the experiment. Correct choices required less time than incorrect ones except in case of Female V, all of whose choices were very rapid.

Male IV	
Time of correct choices	average 28 seconds.
Time of incorrect choices	average 30 seconds.
Female V	
Time of correct choices	average 18 seconds.
Time of incorrect choices	average 17 seconds.
Male V	
Time of correct choices	average 31 seconds.
Time of incorrect choices	average 47 seconds.
Female VI	
Time of correct choices	average 1 min. 20 seconds.
Time of incorrect choices	average 1 min. 49 seconds.

Female V made the quickest choices and gave the poorest results. Male IV gave the best results and made rather hasty judgments. Female VI gave the next best results and was the slowest of them all in making her choices.

It is noticeable that, with one exception, the time required to make the choice was shorter for the correct choices and longer for the incorrect choices. This coincided with the opinion of the human subjects.

However, there were too few birds experimented upon to draw any definite conclusions as to the relation of the time required to make a choice and the success or failure of the judgment. This is a most interesting problem for further investigation.

TABLE VIII

All records for the day before and the day after a forty-eight hour interval. The day before was usually Saturday; the day after Monday. The average for the day after is in every case greater than that for the day before the long interval.

Male IV		Female V		Male V		Female VI.	
Per Cent of Error		Per Cent of Error		Per Cent of Error		Per Cent of Error	
Saturdays	Mondays	Saturdays	Mondays	Saturdays	Mondays	Saturdays	Mondays
0	6	0	6	60	40	90	90
13	6	13	0	33	46	10	40
0	0	6	6	0	0	20	40
0	0	0	20	0	13	30	0
0	0	13	6	6	0	0	0
0	53	0	33	26	13	6	13
46	60	60	26	20	26	13	0
40	33	40	26	20	33	0	0
33	26	26	46	26	26	6	0
0	0	26	46	20	26	46	26
33	26	20	33	26	13	0	20
6	53	33	13	20	13	13	20
0	26	0	26	20	40	20	20
26	26	26	40	40	40	6	0
26	26	33	33	46	46	0	0
26	20	0	46	13	33	13	6
26	20	46	13	13	0	0	20
33	20	0	20	26	26	33	20
26	0	0	13	0	13	13	26
40	53	0	0	0	0	26	20
40	53	33	0	20	40	6	33
33	20	6	40	13	0	13	26
20	46	40	33	33	40	26	20
40	46	20	33			26	26
53	46	20	13			13	0
40	53	13	26			0	20
46	33	0	20			0	26
33	46	20	26			13	20
46	6	26	13			33	20
53	33	13	26			20	40
40	53	26	0			40	13
53	33	13	20			0	26
33	33	13	20			0	6
13	26	26	40			0	0
		0	26				
		6	6				
		6	13				
		0	26				
		0	0				
Ave. 26.97	Ave. 28.8	Ave. 15.81	Ave. 21.35	Ave. 20.91	Ave. 21.91	Ave. 15.73	Ave. 18.73

Difference between Saturday and Monday record.

1.83	5.54	1.00	3.00

(f) Effect of 48 hour interval between successive series. Table VIII shows the effect of 48 hours interval between successive series. As stated before, one series per day was given each bird except on Sunday and an occasional holiday. So this table gives the percentages of error for the series on the day preceding the holiday and the percentage of error for the day succeeding the holiday. In a few cases the position of the variable was changed over the holiday and so these cases were not considered.

For Male V the average percentage of error for Saturday and days preceding holidays is 26.97, while for the day following the 48 hours' rest, his percentage of error is 28.8 or an increase of 1.83%. For Female V the average percent of error for Saturday, etc., is 15.81% and for Monday the average is 21.35%, which shows an increase of 5.54%. Male V has an average per cent of error on Saturday of 20.91% and on Mondays an average per cent of error of 21.91%, which is an increase of just one per cent. Female VI has an average per cent of error on Saturdays of 15.73% while on Mondays her average per cent of error is 18.73%, which shows an increase of three per cent.

To recapitulate: For Male VI Mondays show an increased percentage of error of 1.83%; Female V, 5.54%; Male V, 1%; and Female VI, 3%. Thus each of the birds shows the effect of an extra 24-hour interval between two series, by an increase in the average percentage of error for the following day.

(g) Persistence of stimulation. It has been the experimenter's observation that the sparrows do not retain the effects of stimulation very long at a time. Frequently, as stated before, the birds would get the position habit of alternating from one side to the other. One day, when this occurred, the series was interrupted as the experimenter was called out of the room. Upon returning to the experiment the observer noticed that the bird hesitated before choosing between the lights. He then chose the same light as in the test preceding the interruption. Then in the following tests he alternated from one side to the other as before. So the alternation was in regular order with the exception of the one break due to the interruption. After that when a bird acquired the habit of alternating from one side to the other, the observer would stop the experiment several minutes. In practically every case the bird would hesitate in making a choice in the test following the interruption and usually this caused a break in the order. It looked as though he had forgotten which light he had chosen before. It would be interesting to experiment further in detail upon this question. But from the very limited material at hand, the observer is inclined to think that the birds do not retain visual impressions very long at a time.

IV. QUESTIONS SUGGESTED BY THIS INVESTIGATION.

The question arose as to whether or not the birds would have reached their threshold of discrimination in less time if the intermediate steps were omitted. That is to say—train the bird to discriminate the lights with wide differences in intensity. Then make the difference very small and see if the bird could not learn to make the discrimination in less time than was required to pass through all the intermediate steps. The observer thinks that a great number of the intermediate steps might be omitted in the earlier part of the experiment when the differences in the intensities of the lights were large. Female VI and Male V were trained to choose the darker of the two lights. Female VI learned to choose the darker of the two lights when they were 162 cm. apart, which made the darker of the two lights very dim. Male V learned to choose the darker of the two lights when they were 60 cm. apart and learned the problem in a shorter time than did Female VI. It might have been better to have omitted all the work with the wide difference in intensity for Female VI and begun where Male V began. The results of Male V might have been due to the fact that the darker of the two lights was not so dark as it was for Female VI. It may have been easier for the bird to learn to choose a light of medium intensity, than it was for Female VI to learn to choose a light of extremely low intensity. However, the small steps seemed to be essential as the birds neared the threshold. In one case the observer decreased the difference in intensity too much by one step. The bird seemed absolutely unable to make the discrimination after it had been at the problem a long time. But when the lights were shifted back to their former position and then the difference in intensity decreased step by step, the bird experienced no difficulty in making even finer discriminations. So it seems that the tests at intermediate intensities were essential and that practice was an important factor in learning.

Another question was raised. When perplexed for a long time does the bird forget or unlearn the problem? The observer is inclined to think that it does.

Male IV learned to discriminate the lights when the difference in intensity was .017 c.p. after 225 tests. The difference in intensity was decreased to .013 c.p. and he learned the discrimination in 315 tests. The difference was again decreased to .009 c.p. The bird was completely perplexed. Each time he went to the right side. 390 tests were given him but he could not learn to discriminate so small a difference in intensity. The variable light was shifted back so the difference in intensity was .013 c.p. He had correctly discriminated this difference before in 315 tests. But now he continued to go every time to the right side. After 360 tests the difference in intensity was again increased—this time to .017 c.p. He had previously learned this discrimination after 225 tests. The bird still persisted in going to the right side. The observer finally decided that the bird had forgotten the problem. So the difference in intensity was made extremely large. The bird correctly discriminated the lights in 15 tests. The lights were then shifted back to .017 c.p. and the bird took 240 trials in learning the discrimination which had only required 225 trials in the descending series. The results therefore, seem to indicate that the bird was perplexed so long that he really forgot or unlearned the problem.

Another question which suggested itself was whether or not the birds would learn the position habit if the order was very complicated. They soon acquired the habit of alternating from right to left. A few times the experimenter observed that the birds learned to go twice to one side and twice to the other and three times to one side and three times to the other. These latter cases might have been merely accidental. It would certainly be an interesting problem to try various orders and see if the bird could learn them. Also, could the bird acquire the position habit if it did not have the light to guide it, i.e., if the lights were of equal intensity?

The observer is very much interested in the question of whether or not these periods of stubbornness or stupidity, which all the birds seem to have occasionally, occur periodically. She was unable to tell from the data at hand.

Before concluding the author wishes to express her deepest appreciation of the valuable suggestions, criticism and encouragement of Dr. M. E. Haggerty, who so kindly suggested and directed this experiment. She is also greatly indebted to Dr. Haggerty, Mr. William O. Trapp and Mr. George H. Hyslop, who were the human subjects in this investigation.

THE ROLE OF RANDOM MOVEMENTS IN THE ORIENTATION OF *PORCELLIO SCABER* TO LIGHT

HARRY BEAL TORREY and GRACE P. HAYS
Reed College, Portland, Oregon

1

In his admirable paper on "The Selection of Random Movements as a Factor in Phototaxis," Holmes[1] has given great significance to random, that is, spontaneous, non-directive movements in the orientation of earthworms, blow fly larvae, and leeches, to light. As he carefully watched the movements of these organisms under the influence of light, it "soon developed that what seemed at first a forced orientation, the result of a direct reflex response, is not really such, but that the orientation which occurs and which is often quite definite is brought about in a more indirect manner by a mode of procedure which is in some respects similar to the method of trial and error followed by higher forms." The organism becomes oriented by following up those random movements which bring them away from the source of light.

While our experiments on the larvae of an undetermined species of blow fly and on a species of earthworm (*Allolobophora* sp.) materially lessen for us the importance of random movements as a factor in the orientation of these organisms to light, our conclusions are in complete accord with Holmes' view that the type of reaction he describes "differs from Jennings' 'motor reflex' by which many of the so-called tropic reactions are produced in the Protozoa." This difference has little significance for Mast[2] who believes that "the only difference between the orienting reactions in the two classes of animals mentioned is that the unicellular forms studied by Jennings always turn toward a structurally defined side, while the metazoa investigated by Holmes are not thus limited in their direction of turning."

---

[1] Journal of Comparative Neurology and Psychology, 1905, No. 15, p. 18.
[2] Light and the Behavior of Organisms, 1910, p. 51.

In thus minimizing a difference to which Holmes has explicitly called attention, Mast may have missed a cardinal point in Holmes' illuminating discussion. The direction of the random movements of the blow fly larvae as observed by Holmes is not predictable so far as it bears no definite relation to the source of light. The direction of the movements of *Euglena*, an organism in which the "motor reflex" plays an important part in its orientation to light, *is* predictable, since it *does* bear a definite relation to the source of light. In the one case, the orienting movements, made at random, are not controlled, as to direction, by the light; in the other case, the orienting movements are definitely controlled, as to direction, by the light. In the former, selection operates among so-called trial movements; in the latter, in so far as the movements are controlled or forced by an external agency, the method of trial is excluded. This difference, then, is of no little significance in an attempt to determine—as this paper is attempting to determine for certain organisms—the actual value of the orientation hypothesis that rests upon the assumption of trial movements.

2

The fact that some authors do not distinguish between random movements and directive movements forced by the environment has been a source of some confusion in the literature of animal behavior. Further confusion has centered about the conception of symmetrical stimulation repeatedly emphasized by Loeb and recently reaffirmed by Parker.[3] Investigators of the orienting reactions of non-symmetrical protozoa or symmetrical organisms such as rotifers and worm larvae that swim, like the protozoa, in spiral courses, have had difficulty in seeing the applicability of this conception to their material. That the conception is applicable, however, to the behavior of such organisms as *Euglena*, though not in the form apparently anticipated by some of its critics[4] a recent paper[5] has attempted to show. And its applicability to the orientation of earthworms and blow fly larvae to light has been convincingly discussed by Parker in the paper just mentioned.

---

[3] Journal of Animal Behavior, 1911, No. I, p. 461.
[4] Mast, 1910, p. 85.
[5] Torrey, Science, No. 38, p. 873.

These conceptions of symmetrical stimulation and of forced directive movements have long characterized the tropism hypothesis, whatever other attributes it may be said to possess; and they appear to be quite inconsistent with the conception of orientation by the selection of trial reactions. There should be little danger of confusion, then, in designating as tropic reactions not only the very gradual turning movements that may or may not be connected with tonic contractions accompanying constant stimulation, but also the more abrupt and angular turning movements composed of a series of forced shock reactions, *all in the same general direction*, that we have repeatedly observed in the orientation of *Euglena* to light. Both extremes are, in fact, represented in the behavior of *Euglena*, which will be considered in another paper. Whether they also represent two different mechanisms of orientation is a question for the future to decide.[6] That they do not involve the selection of random movements there appears to be no doubt.

In the following account of the reactions of *Porcellio scaber*, it will be seen that although random movements are common they can readily be distinguished from the forced movements that occur in definite predictable directions in response to differential stimulation of symmetrically situated photoreceptors. But such phototropic movements not only exist; they are *large factors* in the orientation of *Porcellio* to light. This is true also for *Allolobophora* sp. and the larvae of an undetermined blow fly.

3

Porcellio scaber, a species of sow-bug, or wood louse, very common on the Pacific coast, is a typical symmetrical isopod with a pair of compound eyes set far apart in the head segment, and two pairs of antennae, of which the second antennae are conspicuous tactile organs, restlessly active during locomotion. The subequal walking appendages and the body in general are also sensitive to contact stimuli. Of other sense organs it is unnecessary now to speak.

---

[6] Since this was written, a paper by Dr. F. W. Bancroft, in the Journal for Experimental Zoology for November, 1913, appears definitely to have settled the question, for Euglena at least, in the affirmative.

During the day *Porcellio* is usually found under stones, logs, rubbish, in dark cellars, and various other sorts of cover from the light of the sun. Correlated with this habit is a definite negative phototropism.

In our first experiments, this phototropism was more or less masked by large individual differences in sensitiveness to light, and the apparent indifference of many individuals to light coming from incandescent bulbs placed directly in front of them. Later we discovered that the locomotion of many such indifferent individuals could be controlled with great definiteness by holding an incandescent bulb behind them, as they marched over a dead black table top, and moving it to one side or the other. Under these conditions—Mazda bulbs of both 25 w. and 60 w. were used—the organisms would move away from the light with the precision of a boat answering the helm. They could be guided in circles, in spirals, in courses that were directed, now to the right, now to the left, at the will of the experimenter.

That the eyes were the organs responsive to light was demonstrated by blinding them with a mixture of charcoal and glue. Individuals with the right eye blinded reacted to light from the left only; when the left eye was blinded light from the right was alone effective; when both eyes were blinded the individuals thus treated were indifferent to light from any direction.

4

Porcellio responds not only to changes in the direction of light. Exposure to light stimulates into activity animals that in darkness are quiescent; though sudden changes in intensity of illumination may produce inhibitory effects. Individuals vary considerably in their responses to these and all other types of stimulation. Marked differences may exist between individuals of the same size and apparently the same age; also between the reactions of the same individual at different times. Age differences are frequently connected with different reactions. Very young, unpigmented individuals are more responsive to directive stimulation than old. It is the rare exception for them to fail to respond, although adults are not uncommonly refractory. To sudden changes in intensity of light, however, old react at least as sensitively as young. In this connection the following case may be cited.

A female with a full brood pouch was placed in a Petri disk, round and round which she proceeded to move in the light of a 25 w. tungsten bulb. Many times when she was facing the light, the latter was turned off. Invariably she came at once to a dead stop. Only occasionally when the light was turned off while she was facing *away* from it would she react similarly; being obviously less responsive in such cases. Sudden *increases* of intensity, (i.e., when the light was turned on) always produced definite inhibition of locomotion.

One of the brood of this female responded but rarely to sudden increases of intensity when facing the light, not at all to sudden decreases and never while going away from the light.

The fact that young are more readily directed in locomotion by light while they appear to be at least no more sensitive than adults to sudden changes in intensity of light. suggests the possibility of two mechanisms governing the two types of reaction. There is a wide variation in the responsiveness of adults to sudden changes in intensity, however. The problem presented here will be investigated further.

5

Though the eyes of *Porcellio* are sensitive to light, their power of forming images is approximately very small. Totally blind individuals avoid obstacles with the ease of normal individuals. When the second antennae of either are removed, however, they often bump squarely into obstructions, avoiding them only after contact through legs or body. The importance of the second antennae is emphasized by their constant activity during locomotion. when, by a rapid succession of tappings on the substratum, and wavings in the air, they explore the region immediately to the front. The usual random movements that are made by the anterior end of the earthworm and blow fly larvae are in *Porcellio* restricted to these mobile antennae. Since the head segment of *Porcellio* does not move perceptibly from side to side, it is only necessary to amputate the second antennae to eliminate what correspond to the usual random or trial movements in earthworm and blow fly larvae.

Such an operation was made in several cases. It was soon found, however, that, with or without the second antennae, *Porcellio* responded to photic stimulation under the conditions of our experiments with unequivocal, definite, tropic reactions. So the operation was discontinued as useless. In later experiments on blow fly larvae and Allolobophora, the same definite tropic reactions were observed.

6

For the sake of clearness it should be pointed out not only that " random movements " and " trial movements " are expressions not always used in the same sense, but that apparently spontaneous random movememts may be controlled to some extent by the environment. The exploring movements of the second antennae of *Porcellio* are largely initiated and regulated by internal conditions; this is evident especially when environmental conditions remain constant. A slight change in the texture of the substratum, however, may produce marked changes in its behavior; in the absence of the antennae, contact differences may make themselves effective upon the path of locomotion through the legs or body. It is a truism that the behavior of an organism is a resultant of the responses to all simultaneously acting stimuli. A movement initiated from within, when the organism is exposed to various contact stimuli, may frequently be modified if not entirely inhibited by them. The same may be said of movements initiated from without.

It happens, therefore, that so-called " trial " movements in *Porcellio* and blow fly larvae and earthworms vary their character and intensity with circumstances. They may be so augmented by external stimuli as largely to obscure the tropic reactions which under other conditions are readily perceived. The source of the external stimulation may, however, be very inconspicuous. This was especially true in the case of a blow fly larvae that had been traveling away from the light in a direct course with very slight lateral movements of the anterior end. Suddenly the anterior half of the body was lifted and swung from side to side, up and down, in irregular movements of large amplitude that continued for several seconds. The cause of this change in behavior was finally discovered in a bit of filament from the paper substrate that had been picked up and was adhering to the anterior end. For the time, these vigorous " trial " movements, initiated probably by internal conditions but owing their conspicuous characters to contact stimuli, effectively masked the heliotropic movements so apparent under other conditions. Similar pronounced movements were frequently seen when a larva, crawling out over the edge of the glass plate on which it was being observed, would free the anterior third or half of its body. It would then wave this free portion about much in the manner of a leech. Dryness of the substratum may produce similar effects. Such behavior suggests the probability that even the small random or trial movements of the anterior end that ordinarily accompany locomotion are controlled—their amplitude, perhaps being determined—to some extent by contact stimuli.

7

It is possible then, to distinguish between random movements that have no connection with photic stimulation, and movements that Mast calls trials, but are conditioned by photic stimulation. For convenience in further analysis, it will be desirable to distinguish between two groups of reactions thus conditioned. In the one may be placed reactions to high intensities of light, such as direct sunlight; in the other, reactions to lower intensities. All of these reactions are regarded by Mast as trial movements similar to the avoiding or shock reactions of the lower organisms. The reactions of the second group—however we may view them as "trials"—do indeed resemble those reactions of such a form as *Euglena*, that are in the *same general direction* with reference to the source of light. The reactions of the first group, however, occur *either toward or away from* the source of light. They are non-directive with reference to the source of light.

This distinction is emphasized by our observations on earthworms and fly larvae. When light was allowed to fall from the side upon the extended anterior end of either of these forms, the first movement of the anterior end was for certain intensities of light *away from* the latter, whether directed toward or away from the light, when exposed.

8

To eliminate as far as possible all non-directive reactions from the behavior of *Porcellio* to light, in order to discover any directive, tropic movements of orientation that might be present, we adopted two very simple methods. The first consisted in exposing sensitive individuals suddenly to lateral illumination. The individual to be observed was placed on a smooth dead black ground, in a dark room. When its orientation had been accurately determined by means of a 25 or 60 w. tungsten bulb a few inches behind it, away from which it was moving, or a distant light in the ceiling, another tungsten bulb of either 25 or 60 w. and at different distances varying between 20 and 40 cm., was suddenly turned on, so that its light should strike the animal from the side at an angle as near ninety degrees as possible. Sometimes at the instant the lateral light was turned on, all other lights were extinguished; at other times, they were not. In both cases, the direction, with reference to the lateral light, of the first movement of the organism out of its course was determined.

These experiments, simple as they were, gave results that were strikingly definite and convincing. *Almost invariably* the first movement was *away from* the lateral light. The reaction was sharper, on the whole, when light came from the side only. To the 60 w. light, at 40 cm., the response was more definite than to the 25 w. light at the same distance. But the reaction was unmistakably negative within the limits of variation of lighting and distance mentioned. A significant feature of the results was the ease with which they were obtained and the simplicity of means employed.

It must be remembered that all individuals are not equally sensitive to light. But the consistency with which many individuals turned *away* from the light, whether the latter was on one side or the other, left no room for doubt that the reaction was *forced in a definite direction.*

9

The second method of experimentation, equally simple, was determined by the fact that many individuals responded more readily to light coming from behind than from in front of them. The following series of observations taken one afternoon are not selected, but indicate the reactions of the first individuals tested.

The lamps used in these experiments gave a source of light 4 to 5 cm. in diameter. This fact it is important to keep in mind when considering the definiteness of the responses of *Porcellio* for the smaller angles of incidence recorded in the tables. For instance, at 70 cm. from the organism the light used possessed an angular diameter of 4°; at 36 cm., 7°; at 50 cm., 6°; at 15 cm., 16°.

I. A 25 w. tungsten bulb gave the light at approximately 70 cm. from the animal. The latter was a medium-sized adult. Since the sexes respond similarly to light, no account was taken of sex in this and the following experiments. Having determined the orientation of the animal by means of a 60 w. bulb behind it, this bulb was turned off as the 25 w. light was flashed upon it, from in front, striking the eyes of the animal so as to make an acute angle with the axis of the body.

Trial 1,	Light	35°	to left	; response to right.
“ 2,	“	15°	“ “	; animal stopped, wavered, and turned to right.
“ 3,	“	70°	“ “	; animal stopped, then turned to right.
“ 4,	“	60°	“ “	; response to right.
“ 5,	“	10°	“ “	; animal stopped, moved forward, then to left (toward light).
“ 6,	“	5°	“ “	; same as 5.
“ 7,	“	3°	“ “	; same as 5.
“ 8,	“	5°	“ right	; animal turned to left.

These trials show a tendency in the organism to turn away from the light, the direction in which the turn is made depending upon the position of the light and the angle at which it strikes the eyes; there is a stronger tendency to turn to the left than to the right, but this is overcome when the light from the left strikes the eyes at an angle with the body axis of 15° or more.

The same tendency to turn more readily to one side than to the other is seen in the next series; though here the organism turns more readily to the right.

II. Another individual. Lights as in Series I.

Trial 1,	Light	10°	to left,	36	cm.	distant.	Response to right.
“ 2,	“	35°	“ “	36	“	distant.	Response to right.
“ 3,	“	5°	“ right,	36	“	distant.	Response to right.
“ 4,	“	12°	“ “	36	“	distant.	Response to right.
“ 5,	“	5°	“ “	70	“	distant.	Response to right.
“ 6,	“	5°	“ left,	70	“	distant.	Response to right.
“ 7,	“	45°	“ right,	70	“	distant.	Response to left.
“ 8,	“	30°	“ “	70	“	distant.	Response to left.

As in the first series, the organism turns *away* from the light, either to the right or left, when light strikes it at an angle greater than a certain magnitude, in this case between 12° and 30°. When the light strikes it at an angle of 12° or less, the organism turns *toward* the light in the definite turning movement that ultimately carries it *away* from the light.

The two series of trials just presented suggest a difference in the sensitiveness of the two eyes to light. Tests of each individual by means of a light shining upon it from behind, fully supported this view. The first individual was guided without fail to the left when the light came from behind at a small angle to the right; but the same individual did not respond with such definiteness to light coming from behind at a similar angle to the left. These statements will apply equally well to the second individual, if the directions are reversed.

III. Another individual, young, unpigmented. Lights as before.

Trial 1,	Light	25° to right,	36 cm.	distant; response to left.
“ 2,	“	3° “ left,	50 “	distant; response to right.
“ 3,	“	3° “ “	50 “	distant; response to right.
“ 4,	“	5° “ “	50 “	distant; response to right.
“ 5,	“	5° “ right,	50 “	distant; response to right.
“ 6,	“	5° “ “	50 “	distant; response to left.
“ 7,	“	8° “ “	50 “	distant; wavered, then left.
“ 8,	“	5° “ “	50 “	distant; wavered, then left.
“ 9,	“	15° “ “	50 “	distant; response to left.
“ 10,	“	5° “ “	50 “	distant; response to left.
“ 11,	“	*en face,*	50 “	distant; toward light, then left.
“ 12,	“	5° “ “	35 “	distant; response to right.
“ 13,	“	5° “ “	50 “	distant; response to left.
“ 14,	“	10° “ left,	50 “	distant; response to right.
“ 15,	“	8° “ right,	50 “	distant; response to left.
“ 16,	“	10 “ left,	50 “	distant; response to right.
“ 17,	“	5° “ “	50 “	distant; stopped, then to left.
“ 18,	“	10° “ “	50 “	distant; response to right.
“ 19,	“	*en face,*	50 “	distant; wavered, then to left.
“ 20,	“	5° to right,	50 “	distant; response to left.
“ 21,	“	5° “ “	50 “	distant; wavered forward.

This series brings out the fact that although the individual responds to light as an approximately symmetrical animal, its reactions lose precision when the light rays fall upon it from the front at very small angles (e.g., five degrees or less) with the axis of the body.

The following record of another individual bears directly upon this point. Preliminary tests showed that this individual, almost symmetrically sensitive to light, responded toward the right a bit more readily than toward the left. A 60 w. Mazda lamp was used, about 15 cm. in front of the animal, a given number of degrees of arc to the right or left as the case might be.

Light	5°	to right;	5	trials.	Responses	to	right,	2;	left,	3.
“	5°	“ left;	6	“	“	“	“	5	“	1.
“	10°	“ right;	6	“	“	“	“	2	“	4.
“	10°	“ left;	5	“	“	“	“	4	“	1.
“	15°	“ right;	7	“	“	“	“	0	“	7.
“	15°	“ left;	6	“	“	“	“	6	“	0.
“	20°	“ right;	6	“	“	“	“	0	“	6.
“	20°	“ left;	5	“	“	“	“	5	“	0.

It appears from these observations that while the initial locomotor response might be toward the light in a small percentage of cases, such responses occurred only when the rays of light made an angle of less than 15° on right or left with the body axis. This is not surprising when one remembers the large angular diameter of the source of light in this experiment. Beyond 15° the response was consistently away from the light. Further, in the few cases when the response was at first toward the light, the animal continued to turn toward the same side until it ultimately moved away from the light. These exceptional cases, then, only emphasized the negative phototropism of *Porcellio*.

SUMMARY

1. Reasons are given for considering every orienting reaction phototropic whose direction is predictable in that it bears a definite relation to the source of light. *Euglena viridis*, species of blow fly larvae and earthworms, and *Porcellio scaber* exhibit reactions of this type, which is not satisfactorily interpreted by the method of trial.
2. *Porcellio* is easily guided in any desired direction by changing the direction of light falling on it from behind.
3. The first locomotor movement made by *Porcellio*, when exposed suddenly to light striking it at an angle of 90° with the major axis, was *away from* the light.
4. The same pronounced negative reaction followed sudden exposure to light from the front at angles between 90° and 15°.
5. When exposed suddenly to light coming from the front at angles less than 15°, *Porcellio* moved with less consistency away from the light; but the reactions were, on the whole, markedly negative. This lack of consistency was referred partly to the relatively large angular diameter of the source of light, partly to demonstrable inequalities in the sensitiveness of the two eyes of certain individuals to light.

MALE DOVES REARED IN ISOLATION

WALLACE CRAIG
The University of Maine

Eight of my Blond Ring-doves[1] have been reared in isolation, being removed from their parents after the age of weaning but long before the age of maturity, and being brought to maturity in cages where, though they could sometimes hear other doves, they could never touch nor see them. The original intention was to rear each dove out of ear-shot as well as out of sight of all others of its species; but since this would require the keeping of each dove in a separate building, with a quarter-mile or more between buildings, it was found to be impracticable. Of the eight doves reared in isolation, the present article will give the history of three males, Jack, No. 22; Billy, No. 23; and Frank, No. 30, and brief mention of the fourth male, No. 39.

Jack, No. 22. Hatched July 17, 1907. Removed from his parents August 17, his 32nd day.

Throughout the autumn and early winter this bird cooed very little. But about the first of February there began a remarkable development of voice and social behavior. The dove was kept in a room where several men were at work, and he directed his display behavior toward these men just as if they belonged to his own species. Each time I put food in his cage he became greatly excited, charging up and down the cage, kahing[2] and bowing-and-cooing to me, and pecking my hand whenever it came within his cage. From that day until the day of his death, Jack continued to react in this social manner to human beings. He would bow-and-coo to me at a distance, or to my face when near the cage; but he paid greatest attention to the hand—naturally so, because it was the only part with which he daily came into direct contact. He treated the hand much as if it were a living bird. Not only were his own activities directed toward the hand as if it were a bird, but he received treatment by the hand in the same spirit. The hand could stroke him, preen his neck, even pull the feathers sharply, Jack had absolutely no fear, but ran to the hand to be stroked or teased, showing the joy that all doves show in the attentions of their companions. Growing up in isolation from all companions of his own species, he gave himself completely to the companionship of human beings.

---

[1] For a general account of the social behavior and life-history of this species, see Craig, W., The Expressions of Emotion in the Pigeons. I. The Blond Ring-Dove (*Turtur risorius*). Jour. Comp. Neurol. and Psychol., 1909, Vol. 19, pp. 29-82.

[2] " Kah " is the name I use for the well-known cry, sounding like a laugh, which has won for this dove its specific name *risorius*.

July 7, 1908, when Jack was almost a year old, I put an end to his isolation. I tested him (and Billy also) with birds of different kinds, to see if he would choose his own kind. The results were positive, but I have discovered a possible flaw in the conditions of the experiment. When I have pigeons of several species, as I have not now, I shall repeat this experiment on species recognition after rearing in isolation.

July 12, 1908, I placed Jack's cage beside the cage of dove No. 19, a virgin female, in order that they might become acquainted. They had seen each other a little during the previous few days. When the cages were placed side by side, each dove at once showed excited interest in the other, and the female repeatedly gave signs of a desire to mate with the male.

July 14, I let Jack into the cage of the female, by opening the doors between the cages, this being the first time since his infancy that Jack has come into contact with another dove. He went into her cage without hesitation, and soon began to peck and chase her. He had long been accustomed to pecking my hand, but now when he made his first peck at a dove and his bill closed on the feathers, he stopped in evident surprise and did nothing more for a few seconds. But ever after this first experience, he tugged and shook the female dove's feathers as an old male does.

On this first day of contact his attitude toward the female was that of cruel pugnacity, never showing any considerable tenderness or eros. I was obliged to close the doors, preventing contact of the two birds, out of mercy to the female. Next morning the two were lying as near together as they could, in their separate cages, in apparent love and friendship. Nevertheless, after four more days of such acquaintance, when on the afternoon of July 18th I again let him into her cage, he was again cruel to her, though he did also nest-call to her. I closed the doors between them after ten minutes. A main reason to be given for Jack's cruelty to the female, is that he regarded me, the human being, in some degree at least, as his mate; the female dove was, therefore, in so far regarded as an interloper, to be attacked and driven away.

But from July 14th, when Jack first came in contact with a dove, he began to divide his attentions between human beings and doves. He ceased to kah and bow-and-coo to me; though until the day of his death he remained as tame as ever, and always pecked the hand that was put in his cage.

In regard to the sexual reaction, Jack's behavior was most remarkable. He never showed this reaction at all, so far as I observed, until he came into contact with another dove. And then he showed (at first) no tendency to unite with that dove. But it appeared nevertheless that the dove had aroused his sexual impulse; for on July 18th, when food was put in his cage, Jack pecked the hand that was putting in the seed-cup, then assumed that peculiar erect posture which precedes copulation, jumped on the hand, and began to go through the movements of copulation, an act he had never done before.

"July 19, 10:40 A. M. I open the doors, letting male into cage of female. He chases her savagely, bites, pulls feathers. After one minute he goes to nest-calling, but soon savagely chases her again.

"He then bows-and-coos a great deal to *me*. Also, he makes a curious little flight upward, and a feint as if to alight on back of female. I suspect that he is seeking copulation, but is seeking the hand as his stimulus; so I put hand in the cage, and find that my surmise is correct. He does not tamely jump on the hand, he flies on it; then he begins to go through the movements of the sexual reaction. Soon as this was put beyond question, the hand was taken away from him."

The male then went back to the nest site, sounded the nest-call, allowed the female to come to him and caress him, preened her head a little in return, and thus worked himself up to another crisis of excitement. When the crisis came, he again made not the slightest attempt at intercourse in the normal manner, but made frequent *flights* upward in the direction of the female, or in other directions, exhibiting high excitement and some bewilderment. "When he flies up he always hovers, sometimes over the female, sometimes over he knows not what." Sometimes he tries to reach me, sometimes not. After such an abortive attempt at venting his passion "he chases the female as savagely as ever, or more so, even jumping on her back. Then they nest-call again. Then he chases her again." They reach the stage of attempting to bill, which stimulates the male so that he dashes up again in his passionate, hovering flight. "Thus they repeat and repeat."

July 20, both forenoon and afternoon, I let the birds come together for a time, with the same results.

July 21, I let the birds come together, and put a nest in the cage. Once when the male was in the nest and the female at the other end of the cage, he "nest-calls to her a few times, then suddenly he lifts himself and glares at her, chases and worries her a long time, even pulling feathers out. Four times during this onslaught he makes one of his peculiar passionate flights; the first three times the flight was toward female, as if with vague notion of alighting on her; the second time he did alight on back of her neck but did nothing more. The fourth time, in contrast, was a flight high (nearly two feet?) in air."

The same day the female began to sit in the nest, preparing to lay. This fact checked the male somewhat in his activity toward her; as it does every male. But the effect on this male was interesting, thus: "Male jumps toward female, then turns toward me, then pecks female, then runs toward me. Gives it up. Soon at it again; drives female off nest and pecks her many times, then tries to get to me, thus back and forth for long period. Apparently it was his failure to reach me that drove him each time to the female; then his contact with her restimulated him so that he wanted to come to me."

The first experience with a nest I shall describe in another article, dealing with many birds. The first egg was laid July 22. Under the influence of the nest, the egg, and the sitting female, Jack gradually succumbed to the brooding impluse and ceased to show erotic activity. All through his brooding he showed a tendency to come off the nest toward any human being who came near, partly in friendship, partly in anger in defense of nest. But even in showing hostility toward us, Jack reacted toward us, not as he would toward other enemies such as dogs and cats, but with the behavior which a normal dove would show toward intruding members of its own species.

The eggs were of course infertile. At the end of the brooding period I separated the pair, and kept Jack in isolation again through the winter. When the spring awakening came upon him (spring of 1909), he directed his display at first to no fixed and definite objects, but a little coaxing started him bowing-and-cooing to human beings, and soon he cooed to us a great deal, though not, I think, with quite the same earnestness as in his first spring season when he had had no experience with a dove mate.

July 5, 1909. For the first time since the previous year, I placed him where he could see another dove—this time dove No. 20, an old, experienced female. The next day he began to show eagerness, evidently erotic, to reach human beings. On July 11th he tried to copulate with the hand. On July 15th, on two occasions, I saw him trying long and hard to accomplish the sexual act on one of the perches of his cage.

July 22, 9:15 A. M.-12:30 P. M. I opened the doors, allowing Jack into the cage of the female. He made no attempt to copulate with her; but at 11:30 A. M. I saw him, by himself, trying as on July 15th to accomplish the sexual act on a perch.

2:15 P. M. Again I open the doors. Soon I see the pair billing. The female, an old experienced bird, takes the lead, assuming the copulation posture many times, but the male does not mount.

2:35. They try again. The male mounts, but fails to accomplish the act.

2:43. They try again. The male does not mount.

2:50. The male tries to get out toward me.

2:58. After long preliminary the male mounts, but too far back and to one side, and he soon dismounts. They bill again, then give it up.

3:07. After billing male begins to go through the sexual reaction on the perch. The female interrupts him by commencing again her begging reaction.

3:10. The male tries to get out toward me.

3:35. They try again, not successfully, I think. After further preliminary reactions, the male makes a slight attempt to perform the sexual act on the perch, but soon desists.

3:50. They make an attempt which is apparently successful.

After this the male quickly learned to copulate with the directness and efficiency which characterize experienced doves.

He went through the process of incubating the eggs and brooding the young. And in March, 1910, he fathered another brood. But he was always liable to leave the eggs or the young whenever a human being came into the room. He was, therefore, a very poor sitter and a poor brooder, and his young were not well fed. Since I was hard pressed for room to keep my birds, I felt I could not keep a bird which was worthless as a parent: I gave Jack to the University of Maine, and he was killed and mounted for the museum.

Billy, No. 23. Hatched September 23, 1907. Father removed October 1. Young removed from mother October 29, his 37th day.

In order to test whether the development of voice in the young dove is at all due to exercise of the voice, I endeavored to prevent this bird from kahing and cooing. I kept him in a room by himself, with a brick apartment building between him and my other doves. and with the room darkened, so far as possible, at night. Kept so for months, he was far more silent than other doves, but he did coo a little, prompted evidently by internal stimuli. On January 6th I took him to a room in the University of Chicago where he could hear one other Ringdove (Jack), and sometimes Common Pigeons; still he cooed but little. The comparative lack of vocal exercise did not, in any way that I could observe, retard or impair the development of his voice.

His display behavior appeared very suddenly; so far as I observed, it appeared within three days, March 2, 3 and 4. Billy gave himself to human companionship as heartily as Jack had done, losing all fear of human beings, and showing all the signs of excitement and joy in our presence.

After his long period of isolation, Billy was introduced to other birds on the same day and under the same circumstances as Jack (see page 122).

In 1908 I did not give Billy an opportunity to mate, as I did Jack, but kept him in a cage by himself. He could always hear other doves about him, but most of the time he was unable to see them. He continued as familiar as ever with his human companions. Even through the autumn he bowed-and-cooed to us whenever he was enticed to do so. His spring awakening began about the 20th of January, and became just as intense as that of the year before, for when his spring fever was at its height he cooed almost incessantly from the time the window shades were rolled up in the morning until the lamps were extinguished at night.

After three months of excitement, however, he seemed to be tiring out. In the month of May he became much more quiet, and toward the end of that month he acted as if he wanted to sit. We gave him a little straw, and he tried to make some use of it, so a few days later, about May 29, we gave him a nest containing an egg. He took quickly to the nest and sat faithfuly on the egg all day, leaving it only to roost each night.

June 1. Fearing that his health may suffer from lack of exercise, I decide to put an end to his sitting. So at 1:30 P. M. I quietly remove the egg from under him. He sits on unconcernedly.

June 4. Though the egg was removed three days ago he still continues to sit. For the first day or two he sat on the empty nest, but now he sometimes sits on the floor, hooking his bill around little pebbles or such objects and pushing them under him as if they were eggs. He is as savage as a broody hen.

June 11. We took the nest out some days ago, but he continues to try to sit. He is still insanely combative.

June 18. I bring Billy into the company of another male dove (Frank), allowing him not only to see the other dove, but to come into contact with him and fight. This puts an end to his tendency to sit.

Billy was not given opportunity to mate until October 8, 1910, when he was more than three years old. On October 8 and 9 I allowed him to enter the cage of female No. 19 (now a bird of considerable breeding experience), whose cage had long been beside his for preliminary acquaintanceship. I watched the behavior of the pair continuously (closing the cage door between them whenever I could not be present), but I kept out of sight myself, in order that Billy might not be distracted by my presence as Jack was.

October 8. Billy was very cruel to the female.

October 9. Little or no cruelty. He responded to the female with mating and nesting behavior. Several times he showed sexual excitement and a desire to fly on something, yet no tendency to mount the female, until—

3:22 P. M. Female comes in again and flies up beside male, and, on her initiative, they bill two or three times. She then takes the copulation posture, maintaining it steadily, close beside the male and parallel to him. This evidently gives the male just the needed stimulus, for after just the normal pause he mounts. He mounts, however, obliquely across her body, and goes through his sexual reaction in that sidewise position, not effecting union with the female.

On October 10th I was not able to be with the birds, and by mistake I left the door open so that they had free access to each other. During that day Billy evidently learned to mate in a manner almost normal; but for a long time (for years, and I think in some degree to the present day) he persisted in a habit of omitting the preliminary ceremony of billing, flying without warning on the back of the female.

Billy now has had much experience, not only with a mate and young but also with a small flock of doves; his attention has thus been drawn strongly toward his own species, people have been kept away from his cage to some extent, and he has practically given up his abnormal attachment to human beings. For a long time he continued to react with more or less excitement to our presence, especially to our hands, but now no such tendency is noticeable. During his almost three years of isolation he developed a most truculent disposition, partly perhaps because he was teased by some persons—this is probably one reason why he so readily gave up human companionship. After a long period of peaceful life with mate and young, his disposition has become very mild. He is a good sitter, brooder, and feeder of young.

Frank, No. 30. Hatched July 24, 1908. Put in isolation about November 10, his 110th day (a late date, due to lack of facilities).

The history of Frank is in general like that of Jack and Billy, but with many differences of detail.

Jack and Billy had been kept in a well-heated room, where several students were at work daily, both forenoon and afternoon. But Frank was kept in a cold room, in the climate of Maine, where he saw no one except myself, and saw comparatively little even of me. These conditions probably account for the fact that Frank was for a long time a silent and shy bird. He never bowed-and-cooed, so far as I observed, until April 8 or 9, which was just after a warm wave had struck the locality, bringing, as it happened, a great wave of migrant birds. On April 10th Frank bowed-and-cooed a good deal. But after a few days he became quiet, and I did not hear this display coo from him again until about May 8. In bowing-and-cooing he always stood at the same point on his perch, facing toward a certain corner of the room, and thus was probably directing his display to some object, though I did not discover what that object was. He never directed his bows to me until a change came over him which I shall now recount.

Since the bird was uncomfortably shy and afraid of human beings, I began about the last of April to starve him mildly and compel him to feed from the hand. He quickly learned to take his seed in this way, and he always jumped on the hand—but not in a friendly manner, often with a few sharp pecks or a blow of the wing. But on May 11th, after jumping on the hand as usual he stood still a few seconds and then, quite unexpectedly, he gave the sexual reaction of the male.

As soon as the bird had performed this act for the first time, his whole bearing and demeanor changed so markedly that he looked like a different individual. Before, I had mistaken him for a female. Now, his form, his pose (tending toward the charging attitude), his movements, and the glare of his eye betokened the male. He kahed and bowed-and-cooed to the hand, and pecked it in amorous fashion, whereas before he had always pecked in an unfriendly manner. And he allowed the hand to preen his neck and even pull the feathers.

From that date on until the next change in him (June 17th) Frank exhibited almost daily the sexual tendency, but he gradually ceased to bow-and-coo, and he relapsed largely into the demeanor of an immature bird.

June 17. I put his cage beside that of Billy, thus allowing Frank to see another dove for the first time since he was put in isolation. The sight of the other bird and the sound of his voice at once wrought a change in Frank like the change he had temporarily undergone on May 11th, but in this case the change was far greater, and was permanent. He was now in a few moments transformed from the meek young bird of indeterminate sex into the strong, aggressive adult male. I should not have recognized him as the same bird. He seemed to become so much larger than before, that it was hard to believe there was not an actual increase in size. Now he not only bowed-and-cooed, uttered the kah of excitement, and charged up and down the cage, but after a half-hour of such display he assumed the nest-call attitude and gave the nest-call coo, which I had never known him to do before.

June 18 and 19. I allowed these two males to come together. They fought with might and main, and Frank worsted Billy.

After these experiences with another dove, Frank readily and persistently bowed-and-cooed to my face and to my hand, as he had not done before. He continued for a long time, even after he was mated, to jump on the hand that fed him, so persistently that he was a nuisance. But though he jumped on the hand he did not show sexual behavior toward it, not after his first contact with the feathers of another dove on June 18th.

July 5. I placed his cage beside that of a female dove. July 22, I opened the doors, allowing the two to come together. Frank showed a gradual leading up to the perfect mating behavior, similar to that of Billy, but more rapid. The most interesting feature was, that Frank sometimes turned from the female dove to bow-and-coo to me. Since then he has had much experience with doves, and has shown chiefly normal behavior. He maintained for a long time, as stated above, a habit of jumping on the hand. In 1910 he was taken from his cage and put, with other doves, in a large room where he ceased to come much into contact with people's hands, but came naturally into proximity with our feet; he developed that year a habit of bowing-and-cooing to one's shoe and then jumping on the shoe. This habit persisted in 1911, when I noticed that he reacted to tan shoes just as to black shoes, and he showed in many ways that he was reacting to the human being, even though his attention was given chiefly to the shoe. Last year and this year (1913) Frank has been kept in small cages which are so arranged that the hand does not need to be put into the cage to put seed in; he has therefore had no contact with hands or shoes, and he has seen much more of doves than of human beings: he has largely, though not entirely, given up cooing to human beings. When I come near his cage, he still shows a desire to get out to me, and jealousy of other doves in my presence.[3] But he is a successful mate and a good sitter, brooder, and feeder of young.

Dove No. 39. Hatched July 14, 1910. Put in isolation September 26, his 75th day. This dove took to human companionship as did the other three. He has not yet been allowed into contact with his own species, but has been used for an entirely different experiment which is not yet completed.

SUMMARY AND CONCLUSIONS

The history of these doves reared in isolation covers a wide range of behavior, and many points of interest, from which I select the following. These conclusions will be confirmed and amplified in other articles, one of which will treat of female doves reared in isolation.

1. Four male doves were reared (after weaning) in isolation, each being unable to see any dove companions.

2. All these doves were for a long time very quiet. In the case of Frank especially, the masculine display behavior did not appear at all until he was socially stimulated; then the display behavior appeared so suddenly as to transform the bird in a few moments. All four doves exhibited more or less of this sudden development of behavior under the influence of new social factors in the environment.

3. The various notes uttered by this species, and all accompanying expressive movements, developed in perfect form in isolated individuals, showing that young doves do not need to

---

[3] August 18, 1913. Today, due to an accident, Frank escaped from his cage. I followed him with an open cage in which I sprinkled tempting seed, but could not induce him to enter. So I carefully approached him from below, and gently raised my hand to catch him. But he, seeing my hand come to him thus, began to show some of the old fascination for the hand, and after several seconds he jumped on my palm. I quickly put my other hand over him, and he was caught.

learn the sounds[4] or gestures of their species by copying older doves. The vocal and gesture reactions are thus, in their motor aspect, very completely and definitely fixed by the innate organization of the nervous system.

4. On the other hand, the innate sensory inlets leading to these reactions must be very indefinite or flexible. For the doves give their cries and their gestures, now to one sense-object, now to a very different object, according to their experience. The four doves herein described, before they were allowed access (as adults) to their own species, gave their social reactions to human beings.

5. The three individuals which, after maturing in isolation, were allowed into the presence of their own species, associated with the other doves with every mark of eagerness and satisfaction.

6. These three gave up their intimate friendship for human beings. But they gave it up slowly and gradually, showing interesting divisions of attention between human companions and dove companions. If they had been encouraged to do so, they would probably have continued indefinitely to display to human beings; and even without special encouragement they remain, probably for life, exceeding tame, unafraid of the human species. This is one example of the importance and lasting influence of the dove's early impressions.

7. The sexual reaction of the male is, in its motor aspect, very completely and definitely provided in the innate nervous organization. But the innate sensory inlet to this reaction is not a complete sensory inlet; it is supplemented by experience.

8. The object to which the dove directs his social behavior becomes a symbol, in some cases it might even be called a fetich, to which he clings tenaciously, and to which he attaches a great complex of reactions. With all four of these doves, the human being became such a symbol; especially the human hand, and in the case of one dove (Frank) the shoe.

9. When a dove performs an instinctive act for the first time, it generally shows some surprise, hesitation, bewilderment, or even fear; and the first performance is in a mechanical, reflex

---

[4] It is true that each of my isolated males could hear other doves, but not such as to serve as a copy. For Jack and Billy could hear only each other; Frank could hear only the faint sound of doves cooing in a distant room; and No. 39 could hear no male dove but only a few females.

style, whereas the same act after much experience is performed with ease, skill, and intelligent adaptation. Thus even those acts which do not show improvement by the formation of associations, show improvement by *facilitation.*

10. In the case of an act in which instinct plays the greater part, and learning by experience the lesser part, especially when the result of experience is merely facilitation, the improvement in the performance of the act may be so rapid that it quickly leads to perfection. To detect the influence of experience or practice, one must observe from the very first performance of the act. To observe the very first performance of the social activities of the adult, one must rear the animal in isolation; and then allow it, while under close observation, to come into contact with another animal.

NOTES

HUNTER ON THE QUESTION OF FORM-PERCEPTION IN ANIMALS

H. M. JOHNSON

Assistant Psychologist, Nela Research Laboratory, National Lamp Works of General Electric Company

In a recent interesting communication, Mr. Hunter[1] calls attention to the need of sharper distinction between the study of form-discrimination and that of pattern-discrimination. He presents the thesis that animals below man and children between certain ages "have only a more or less crude pattern vision," and are unable to discriminate forms. Mr. Hunter asserts that there is no means of testing the validity of his belief unless the surroundings of discriminable forms be changed, since the form is "seen" with its surroundings and hence must be considered as "part of a pattern." Even if no other objects are in the visual field, the stimulus-object "is seen surrounded by the more or less irregular outline of the field of vision, and so is again part of a pattern." As a means of controlling the surroundings, he proposes that after form-discrimination has apparently been established, the alleys of the Yerkes experiment-box leading to the stimulus-forms be enclosed with hollow cylinders or hollow triangular prisms. Thus, he says, "it should be possible to demonstrate experimentally whether the subject was reacting to the 'forms' or to the 'patterns.'"

I am not clear as to two points raised in reading Mr. Hunter's article. First, with reference to his proposed method of control: Changing the enclosures of the alleyways would probably introduce new olfactory stimuli, and if the animal should have to touch any of the walls, the change would certainly introduce new tactile stimuli. The introduction of any new stimulus-factors frequently works serious disturbances. Quite recently Mr. Lashley[2] reported disturbance from the first source. Mr. and Mrs. Watson[3] obtained disturbance from both the first and second factors. Other instances might be enumerated. Suppose an experimenter should obtain failure to discriminate after making such a change as Mr. Hunter suggests. Is there any means of deciding whether the disturbance resulted from the change of "pattern" or from the simultaneous introduction of other novelties?

---

[1] Hunter, Walter, S.: The Question of Form-Perception. This journal, vol. 3, 1913, pp. 329 ff.

Secondly, with regard to the necessity of any control, which Mr. Hunter assumes: If a human observer place his eye at the exit of the "home-compartment" of the Yerkes box, will not a given form appear against quite different backgrounds and behind quite different foregrounds according as it occupies the right and the left positions respectively? To the writer it does. Since the stimulus-form is as effective in one setting as in the other it would seem that we are justified in saying that the animal is reacting to the constant form difference and disregarding the variable pattern-difference of the stimuli; using the term pattern-difference in Mr. Hunter's way.

---

[2] Lashley, K. S.: Visual Discrimination of Size and Form in the White Rat. Ibid., vol. 2, 1912, pp. 310 ff.

[3] Watson, John B. and Watson, Mary I.: A Study of the Responses of Rodents to Monochromatic Light, Ibid., vol. 3, 1913, pp. 1 ff. The disturbance referred to is not reported, having occurred in the preliminary work. The writer received the information directly from the authors and refers to it with their permission.

A DEFINITION OF FORM

HAROLD C. BINGHAM
Ellsworth College

Regarding separate studies in form perception by Lashley and myself,[1] the following criticism has been urged:[2] " Both series of experiments referred to above are concerned with *patterns*, not *forms*." " In problem boxes such as those described by Lashley and Bingham . . . the animal tested is confronted *not* by two "*forms*" corresponding to the configurations of the opal glass, but by such designs as are suggested in figure 1.

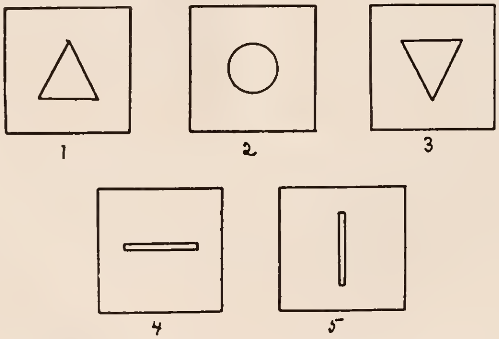


FIGURE 1. Reprinted from *Jour. Animal Behavior*, vol. 3, no. 5, p. 331.

The squares drawn in the figure represent the rectangular tunnels down which the animal goes in making his responses. What the animal sees is a triangle or a circle each in more or less of a square setting." In substance, the form is not without a perceptible environment and, therefore, is strictly a pattern.

Accepting the definition of pattern and conceding for the moment the definition of form urged by Hunter, I maintain that, under the conditions as described in my paper,[3] the visible stimuli presented to the animals for discrimination were forms *not* patterns. On page 66 I state that the whole apparatus was set up in a dark-room. I follow this with an explanation of the only sources of illumination. On page 98 appears the plan of controlling all light factors. Now, in these conditions of control, there is to be found a refutation of the point which Hunter seeks to establish. The rectangular tunnel, to be sure, remains, but the perceptibility of the environment is wholly changed, if not destroyed. That the animals could not see the environment is attested by the fact that they were frequently observed to walk blindly into the confining walls. Not all of the time was the environment "darkened," but the control tests were always made to determine whether or not, among other factors, setting was a factor in discrimination.

---

[1] Lashley, K. S. Visual Discrimination of Size and Form in the Albino Rat. *Jour. Animal Behavior*, 1912, vol. 2, No. 5.

Bingham, H. C. Size and Form Perception in *Gallus Domesticus*. *Jour. Animal Behavior*, 1913, vol. 3, No. 2.

[2] Hunter, W. S. The Question of Form Perception. *Jour. Animal Behavior*, 1913, vol. 3, No. 5, pp. 330–1.

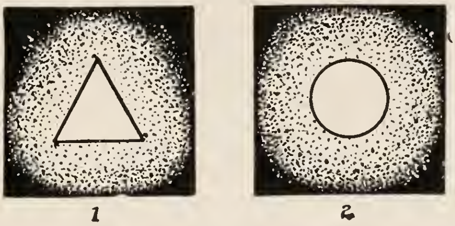


FIGURE 2

Figure 1 does not accurately illustrate the condition of the stimulus areas. With the introduction of a screen between the general illumination and the electric boxes and with the reduction of the intensity of the source lights, a condition similar to that illustrated in figure 2 appears. In the compartment where the triangle appears, the source light fails to illuminate the corners of the tunnel, and so the perceptible portion of the setting changes to a sort of circular form as in diagram 1. About the circular stimulus the visible setting is more nearly a perfect circle as is shown in diagram 2. Even if my apparatus offered a possibility of pattern discrimination, my plan of control would have made so variable the patterns confronting the animal that they never could have served as a basis of discrimination.

Hunter has apparently missed one of the essential features of the apparatus which was used in my study. The dark-room apparatus allows the experimenter to control the conditions of setting by means of artificial illumination. His criticism would be valid for similar experiments conducted in natural and uncontrolled light. With the visual discrimination uninfluenced by setting, the perception could not have been of patterns.

---

[3] *Op. Cit.*

Another feature which Hunter has overlooked is one of method. Referring to figure 1, he asks:[4] "If an animal is trained on diagrams 1 and 2, is it any wonder that he breaks down when confronted by diagrams 2 and 3?" Assuming now that the animal actually sees "a triangle or a circle each in more or less of a square setting," no explanation is offered for the breaking down of the discrimination when merely the size of the form was changed, *i.e.*, when the triangle of 1 was a circumscription or an inscription of the circle of 2. (Witness table 8, series 12, 13 and 14, March 21-22, and series 10, March 28; also table 9, series 5, April 21).[5]

Now in these tests the patterns remained the same except in size, but the reactions changed from a high percentage of correctness to a relatively low percentage.

Besides this mis-statement of conditions there is an obvious lack of agreement in the matter of defining "form." The so-called "abstract sense" in which I have used the term has called forth objections.

In my study of form perception I was not concerned with genetic phases of the problem. My task demanded an answer to the question: Does the chick perceive forms?[6] Consequently, it makes no difference whether or not the conception of form, to which I have given expression, is the result of development. One might consider that phase of the subject, but in my problem I was justified in determining whether or not the chick perceives form in this "abstract sense."

Now if our animals fail to perceive circularity and triangularity as such, there are several principles that we should not lose sight of. In the first place, we should not try to excuse our animals nor become over-dogmatic in theorizing about extraneous, or even allied problems. We should accept as a fact the conclusion to which the evidence points.

Moreover, we should seek to determine and define just what elements our animals *do* perceive. In this task we need not speculate on the question whether such elements are logical or genetic precedents of form perception.

---

[4] *Op. Cit.*, p. 331.

[5] *Jour. Animal Behavior*, 1913, vol. 3, No. 2, pp. 106 and 109.

[6] The task would have taken on other complexities had positive results been secured in the initial problem.

To avoid confusion, we should avoid the application of a multiple meaning to the same terminology. We should not attempt to simplify our definition of form so that this factor may be included in the animal's stock of perceptual experiences.

Finally, if we find that our animals have a power of discrimination which approaches form perception, but which is *not* form perception in the strict sense of the term, we should adopt a terminology to fit the special case; we should not enlarge the conception of the term " form " to cover the special case.

Perhaps " a more or less crude pattern vision " is the nearest approach to form perception that animals possess. At any rate, Hunter has done well in calling attention to the distinction between patterns and forms. However, our definition must not stop here. Two forms may be identical, but different in " shape." This would be the condition in Lashley's study. He used two identical forms in that both were rectangles 2 mm. by 60 mm. They differ in this respect: one is extended laterally thirty times as far as its vertical extension, while the other is extended vertically thirty times longer than laterally. Now this is a difference in " shape " of two identical forms.

Miss Washburn, in reviewing my study,[7] has failed to make this distinction between form and shape. She says: " Bingham's chicks discriminated between a circle and a triangle when the apex of the triangle was on top, but since this discrimination broke down when the circle was presented with a triangle whose base was uppermost, the chick failing to choose the triangle, Bingham concludes that the chick was not reacting to form difference, but to 'the unequal stimulation of different parts of the retina.' The reviewer would conclude rather that the chicks were not possessed of an abstract idea of triangularity. A triangle with apex up is a different form from a triangle with apex down: the two have in common only the abstract quality of three-sidedness. The perception of form, as distinct from an abstract idea of form, is based precisely on the unequal stimulation of different parts of the retina."

---

[7] Washburn, M. F. Recent Literature on the Behavior of Vertebrates. *Psychological Bulletin,* 1913, vol. 10, No. 8, p. 320.

It is not to be denied that a triangle with vertex up differs from a triangle with vertex down. But we can scarcely say that they are two different *forms.* They are both triangles; yes, more than that: they are equilateral triangles. Where they differ is *not in form but in shape.* When the extended base of the triangle is so placed as to stimulate the region of the retina which was formerly stimulated by the vertex of the triangle, a condition occurs similar to that pointed out regarding Lashley's "forms:" the forms remain identical, but the lines of maximum and minimum extension have interchanged. This fact led me to conclude in my paper [8] that *the apparent reactions to forms are the result of keen perception of size differences.* I might have said they are due to perception of shape differences. The inversion of the triangle causes certain particular size changes—vertex or point interchanged with base or line—which causes a change in shape, but no general change of size since the area remains constant. Similarly the factor of triangularity remains constant and the form is unchanged. Not "the perception of form," therefore, but the perception of shape "is based precisely on the unequal stimulation of different parts of the retina."

Our definition, then, as separate from the distinction between forms and patterns, must draw a line between forms and shapes. Referring to the retinal area stimulated, there is form which is general, *e.g.*, triangle. But there is a particular feature about this general distribution of light—it is equilateral, or isosceles, or right angled—viz., shape. Forms are identical when their areas are equal and their general retinal distribution is similar. Shapes are identical when all extensions of the identical forms are equal and in the same relative directions. Thus, the area remaining constant, either or both form and shape may change. The form remaining constant, the shape may change. Change in form must always cause change in shape.

Subsequent studies in this field should not fail to consider the factors of "shape" and "pattern" in their relation to form perception. Whatever system of control is adopted, such possible disturbances as these factors must be considered and, as far as possible, eliminated and isolated. Unquestionably my final test for form discrimination by shifting the position of the form was a severe one. Surely the factor of shape was a disturbing influence. If, with all possible disturbing factors properly controlled, this test of shifting fail, form perception in the strict sense of that term can scarcely be said to prevail.

---

[8] *Op. Cit.*, p. 110.

I have shown that the discrimination of patterns was impossible in my study. There was a possibility of discrimination on the basis of two other factors. One of the remaining factors was form: the other has been arbitrarily termed shape. The inverted triangle possessed a different shape but an identical form as compared with the upright triangle. The high percentage of correctness in reactions changed to a relatively low percentage with the inversion of the triangle. Obviously, then, form was not the basis of choice.

THE AUDITORY REACTIONS OF THE DOG STUDIED BY THE PAWLOW METHOD

SERGIUS MORGULIS
Biochemical Laboratory of Columbia University, New York

From the time the first review[1] of Pawlow's ingenious method in animal psychology was published in this country great progress has been made by the numerous students of Professor Pawlow which puts an entirely new aspect on the psychology of the dog. Unfortunately, we are not in a position at this moment to offer a further extensive summary of the results obtained by this method since 1909, but a brief review of the recent paper of Usiewitch,[2] concerning the auditory faculty of the dog may prove of interest to American investigators.

It will not be amiss to state succinctly for the benefit of those not familiar with the first article referred to, the principle of Pawlow's method, the minute analysis of the animal reactions performed with its aid and some of the broad generalizations regarding nervous activity deduced from those analyses.

It is a matter of common experience that the salivary reflex may be actuated by the mere thought or even remote suggestion of a delectable article, but it remained for Pawlow's unusual acumen to recognize in this trivial fact the means provided by nature for penetrating the hidden workings of the animal's psychology. The presence or absence of the salivary reflex informs the investigator of the organism's reaction to a given stimulus. The method, therefore, possesses all the advantages of being strictly objective, i.e., quite independent of the observer's interpretation or "persönliche Ueberzeugung," as the Germans name it.

Starting with the idea of the salivary reflex, it was a relatively simple matter to determine the flow of saliva both quantitatively and qualitatively by a special adaptation of the Pawlow fistula method. The duct of the parotid gland is exposed by an incision of the cheek and a permanent fistula or outlet to the exterior is made. The saliva is collected in a tube where it can easily be measured.

---

[1] Yerkes, R. M., and Morgulis, S. The Method of Pawlow in Animal Psychology. *Psychol. Bull.*, vol. 6, pp. 257-273, 1909.

[2] Usiewitch, M. A Physiological Investigation of the Auditory Capacity of the Dog. *Bull., St. Petersburg Military Medical Academy*, Vol. 24, pp. 484-502; Vol. 25, pp. 872-891, 1912 (Russian).

Through persistent training the salivary reflex may become coupled with any desired stimulus which is frequently applied while the secretion of saliva is called forth by feeding the animal a powder consisting of meat and sugar. After long continued repetition the application of the particular stimulus alone is sufficient to cause a normal flow of saliva. This indirectly produced salivary reflex is what Pawlow terms a "conditioned reflex," and the success of the analysis of reactions is based upon the absolute specificity of the latter. The ability of the animal to differentiate between gradients of various stimuli is measured by the changes registered in the fundamental salivary reflex.

What the experimenter achieves by patiently adhering to a prearranged plan happens in nature continuously. The world of the individual is two-fold in its make-up. Some of its elements act on the animal's receptors causing sensations by directly stimulating them, others exert an influence, thanks to a more or less temporary association with one of the fundamental or unconditioned reflexes. In the function of the higher centers Pawlow distinguishes, therefore, two mechanisms; the mechanism of receptors ("analysers" in Pawlow's terminology) which is for sifting out and selecting from the mass of external stimuli and transforming them into nervous processes of purposeful reactions; the other mechanism is that of the transitory association or interlocking of the phenomena of the outside world with the organism's responses. The latter is the mechanism of the conditioned reflexes in all its complexity.

One of the most important discoveries in the investigation of the conditioned reflexes is the fact that every receptor at first enters into temporary association with the salivary reflex by its most generalized activity, its more refined and subtle faculty of differentiation being involved only gradually and by a very slow process. The intensity of an illuminated area becomes the cause of a conditioned reflex much sooner than the shape of that area. Likewise, when the central portion of the receptor mechanism—which may be either in the brain or in the spinal cord—

is destroyed or injured this particular receptor loses its ability to form conditioned reflexes except by its primitive and generalized function. Animals whose optic centres have been injured can still form associations between stimuli of various light intensities and the salivary reflex, but not with stimuli from special groupings of light and shadow.

As regards the auditory reactions of the dog it has been discovered by the conditioned reflex method (Selionyi, Elliasson, Tichomirov, Babkin, Burmakin) that its auditory faculty is much greater than that of man. The dog perceives $\frac{1}{8}$ of a tone and appreciates tones of a frequency of vibration which is entirely beyond human reach. It was also discovered that the dog has an absolute memory for sounds, which probably, but very few of the most gifted musicians possess.

Usiewitch's particular problem has been to study the dog's reaction to an intermittent auditory stimulation with a view to determining its ability to differentiate time intervals. It is hardly necessary to describe his technique, which is essentially the same as already described in the review alluded to. The intermittent stimulation was produced by means of a metronome. The subject of these experiments, a large healthy dog which never had been used for similar tests before, was found to be totally indifferent to the metronome so far as its salivary reflex was concerned.

By persistent training a conditioned reflex has been established to the stimulation with 100 oscillations per minute of the metronome. The stimulation of intermittent sounds of such frequency called forth 6-10 drops of saliva every time. The interval between successive oscillations was then modified, the moment of the disappearance of the conditioned salivary reflex indicating the lowest limit of differentiation. Without going into any details of this most interesting investigation or quoting actual data, I will say that the dog could sharply distinguish the shortening of the interval by less than $\frac{1}{40}$-$\frac{1}{43}$ of a second. Indeed with the well developed reflex to the stimulation of 100 beats per minute a change of the rate to either 96 or 104 beats was immediately reacted upon by a marked diminution or even complete cessation of the flow of saliva.

Furthermore, Usiewitch brought out some very significant points with regard to the intermission between tests with the established, standard stimulation, and some unusual stimulation. Thus, the dog is able to differentiate distinctly between 104 and 100 beats (standard) if the new rate is tested 10, 15, 45, or 60 minutes later. The differentiation is less certain after 18 hours of intermission and vanishes completely after a lapse of 45 hours.

In responding to various intermittent stimuli of unaccustomed frequency a remarkable regularity and uniformity stamps the results. Applied immediately after stimulation with the standard rate of oscillation it produces a distinct depressing effect on the salivary secretion in the first trial. During the subsequent few trials the conditioned salivary reflex increases considerably, then again diminishes to complete disappearance in further tests. These facts are very important because they offer a clue to the analysis of the phenomenon of inhibition.

This review purports to bring once more before the attention of American investigators the enormous value of this purely objective analytical method in animal psychology and to stimulate an active interest in the subject which should soon lead to a systematic investigation of the reactions of various animals by this method.

JOURNAL OF ANIMAL BEHAVIOR

Vol. 4 MAY-JUNE, 1914 No. 3

CONSPICUOUS FLOWERS RARELY VISITED BY INSECTS[1]

JOHN H. LOVELL,
Waldoboro, Maine

There are many cultivated flowers adapted to winged pollinators, which are rarely visited by insects although they are of large size and display the most brilliant hues. Among the species enumerated by Plateau as illustrations are the red geranium (*Pelargonium zonale* Willd., hybrid Lepidopterid flowers from Southern Africa), the scarlet sage (*Salvia splendens* Sellow, ornithophilous, from Brazil), the cardinal flower (*Lobelia cardinalis* L., ornithophilous, from North America), and the splendid gaudy flowers of *Passiflora incarnata* L. (probably ornithophilous,[2] from North America).[3] Other neglected flowers employed by Plateau for experimental purposes were *Lilium candidum* L. (hawk-moth flowers), *Passiflora adenophylla* Masters (?), (probably a hybrid), *Œnothera speciosa* Nutt. (hawk-moth flowers), *Pisum sativum* L. (almost invariably self-fertilized, probably introduced from Western Asia into Europe in prehistoric times),[4] *Pelargonium zonale* Willd., *Clematis Jackmanni* Jack. (hybrid pollen flowers), and *Petunia hybrida* Hortul. (hybrid, the South American species are ornithophilous?). That anthophilous birds and insects have played an important part as pollinators in the phylogenetic history of the flowers enumerated, in the lands where they are or were endemic, will not be questioned by any orthodox floroecologist. But manifestly when they are cultivated in widely separated stations, under the most diverse conditions, there is a strong probability that in many localities their normal pollinators will be entirely absent or extremely rare; while the flowers themselves modified both in form and function by artificial selection and hybridization may cease to remain equally attractive, e.g., double flowers may be devoid of both nectar and pollen. On the other hand why should we expect common Hymenoptera and Diptera frequently to visit flowers from which they can not legitimately obtain nectar, and to which they are not beneficial; or why should we look for diurnal insects as common visitors to crepuscular flowers? One of the advantages of reciprocal adaptation between flowers and their pollinators is the exclusion of injurious and useless forms.

---

[1] The pollination of green or inconspicuous flowers has been considered by the writer in an earlier paper. *Am. Nat.*, **46**:83–107, 1912.

[2] In Alabama Trelease saw the flowers visited by humming-birds. Knuth, Paul, "*Blütenbiologie,*" **3**: 510.

[3] Plateau, F., "Les insectes et la couleur des fleurs," *L'Année Psychologique*, **13**:72.

[4] De Candolle, A., "Origin of Cultivated Plants," p. 329.

But Plateau assumes that all bright-hued flowers, according to the theories of Müller and Knuth, no matter what their manner of pollination, should frequently be visited by diurnal insects. The rarity of insect visitors to many beautiful flowers with very showy colors, he remarks, places the biologists of the school of Hermann Müller in a singularly embarrassing position.[5]

He summarizes his views as follows:

" My observations establish the truth of the fact, well-known though not sufficiently insisted upon, of the existence of many plants with flowers formed on the entomophilous type and presenting large dimensions as well as brilliant colors, which attract almost no diurnal insects.

It follows that the attractive rôle, or, as it is often called, vexillary rôle of the forms and colors of floral envelopes is either nul or of very little importance.

Causes of attraction other than colored surfaces are necessary to bring pollinators to flowers and to lead them to return again after a first visit; they are an odor, which is agreeable to the insects, and a sweet liquid, which permits them to appease their hunger and provide food for their young.[6]

Unfortunately for the general acceptance of Plateau's conclusions, they are not of universal application, but are controverted by the characters of various natural flowers. The cornflower, (*Centaurea Cyanus* L.), *Gentiana acaulis* L., and several other gentians have conspicuous nectariferous flowers, which are visited by numerous insects although they are devoid of scent. Bees frequently gather pollen from poppy flowers, which are not only nectarless but possess a faint unpleasant odor. From the wind-pollinated, purple flowers of the elm, which are both nectarless and odorless, honey-bees in immense numbers sometimes procure pollen for early brood-rearing; while many other anemophilous species are also valuable to the bee-keeper as sources of pollen. Nor is it stated that there are many conspicuous flowers, which are neglected by insects notwithstanding they are strongly odoriferous, as the sweet pea, *Lilium candidum*, and varieties of *Pelargonium*, which have the entire plant pleasantly scented. Finally, if a flower is rich in nectar, it may be both inconspicuous and odorless and yet receive numerous visits. According to Fritz Müller, there is in South Brazil a species of *Trianosperma* which is visited very abundantly all day long by *Apis mellifera* and species of *Melipona*, although the flowers are scentless, greenish and to a great extent hidden by the foliage.[7] It is thus apparent that the visits of insects in large numbers are not dependent on the presence of an agreeable odor.

---

[5] Plateau, F., " Recherches expérimentales sur les fleurs entomophiles peu visitées par les insectes rendues attractives au moyen de liquides sucrés odorants," *Mem. de l'Acad. roy. de Belgique*, 2me sér., 2:5, 1910.

[6] *Loc. cit.*, pp. 51–2.

But, assuming the validity of his conclusion that bright coloration is without significance because certain conspicuous flowers are commonly neglected by insects, Plateau performed a long series of experiments, in some instances introducing honey and in others odoriferous sweet syrups into neglected flowers with the result that in most cases insects were attracted, often in large numbers. In his earlier experiments of 1897, he employed only honey diluted with water. When a small quantity of this mixture was placed on the handsome flowers of *Pelargonium zonale*, *Phlox paniculata* and *Anemone japonica*, it was speedily discovered by numerous Diptera and Hymenoptera. Similar results were obtained with greenish or dull-colored flowers. The vexillary organs are, therefore, asserted to be of little or no importance.[8]

Knuth considered these experiments of no value since " they only prove that the odor of honey exercises a great power of attraction which has long been known. It is only necessary to place honey anywhere to secure the immediate appearance of numerous insects which are fond of it."[9] To this criticism, Plateau replied:

---

[7] Müller, H., " Fertilization of Flowers," p. 270.

[8] Plateau, F., "Comment les fleurs attirent les insectes," 3me part., *Bull. de l'Acad. roy. de Belgique*, **33**:27–37, 1897; 4me part., loc. cit., **34**:604–10, 1897.

"Quelle pauvre argumentation! Knuth ne s'aperçoit pas qu'il me donne pleinement raison. En effet, s'il a suffi de l'introduction d'un peu de miel dans des fleurs habituellement négligées pour y amener les Insectes, c'est que l'éclat des corolles ne compte guère et que le perfum de la substance que ces animaux recherchent avidement a constitué seul l'excitant déterminant leurs actes. J'avais donc démontré ce que je voulais démontrer."[10]

Plateau's conclusion that certain conspicuous flowers, which are devoid of nectar and pollen, or nearly so, are neglected because insects fail to notice their colors, it is believed, can readily be shown to be fallacious. The flowers are neglected not because they escape attention, but because anthophilous insects have learned from experience their inability to procure food materials from them. They do not neglect them entirely, but visit them occasionally,[11] although they do not often repeat their futile visits since "memory appears to replace both odor and color as the directive stimulus of first importance.[12] In his experiments with odoriferous essences, that is, odors without a sweet syrup, Plateau recognized the fact that if they are employed alone a Hymenopteron or Dipteron entering the corolla and finding nothing will not return again.[13] This statement is equally applicable to color. Neither color nor odor separately or together will attract insects continuously, if they can obtain no spoil.

---

[9] Knuth, Paul, "Handbook of Flower Pollination," translated by J. Ainsworth Davis, **1**:206.

[10] Plateau, F., "Recherches expérimentales sur les fleurs entomophiles," etc., p. 8.

[11] This statement will be supported later by a large number of observations.

[12] Coulter, Barnes and Cowles, "Textbook of Botany," 2 (Ecology by H. C. Cowles) :850. On the memory of honey-bees cf. Forel, A., "Ants and Some Other Insects," translated by W. M. Wheeler, p. 28; and on the memory of place in bees cf. Buttel-Reepen, H. V., "Are Bees Reflex Machines," translated by M. H. Geisler, pp. 19–39. In the autumn of 1912 I placed a dish containing fragments of comb honey in a secluded spot nearly surrounded by a steep bank and willow bushes. A few bees were brought to the honey and it was soon visited by a large number. After they had been fed several times the dish was removed and everything left as at first. Two weeks later I examined the place but failed to discover a single bee. The weather was, moreover, growing colder and they were no longer flying freely. I now placed on the same spot as previously another dish of comb honey; and two hours afterwards I found it swarming with bees. During two weeks they had evidently kept this locality under constant surveillance, inspecting it from time to time, although there was nothing to attract their attention.

[13] Plateau, F., "Recherches expérimentales," etc., p. 10.

Plateau was equally mistaken in supposing that the addition of an agreeable odor is indispensable; for it is only necessary to introduce a solution of sugar and water, which is odorless, to bring insects to the flowers in great numbers, as will be shown experimentally. In the absence of accessible food materials pleasantly scented flowers will not be visited more frequently than would be the case if they possessed only bright coloration. Insects will not repeatedly visit an inflorescence because they experience an aesthetic pleasure. This is well shown by *Lathyrus odoratus* L., or the sweet pea, which, notwithstanding its strong fragrance and brilliant hues, is very rarely sought by insects, because the nectar is inaccessible to nearly all of them. An ample, available food supply will alone secure continued and frequent visits of insects to flowers. Since it can be shown, therefore, that an inflorescence can be rendered very attractive to insects without the addition of an odor, it logically follows from Plateau's own method of reasoning that conspicuousness is beneficial.

When Plateau introduced honey into certain selected flowers, they received two allurements, an agreeable odor and a sweet liquid food, which sharply distinguished them from the flowers left in their natural state. In effect, the flowers containing honey became distinct physiological varieties. Color and odor were not brought, therefore, into competition on equal terms; the flowers in their natural state possessed only color and form, while those into which honey was introduced possessed color, form, an agreeable odor and a liquid food. Manifestly, the latter flowers were given the greater advantage, and it is unfair to conclude that because they received the greater number of visits, odor was essential and color was of no significance. Throughout Plateau's experiments, the presence of the vexillary organs was a source of error. As he had assumed that they were of no value, it is difficult to understand why he did not remove the floral envelopes, when the flowers would of necessity have been compelled to depend wholly on the odoriferous liquid food. Finally, to have made the competition impartial, an odorless syrup should have been introduced into the empty flowers. The experiments were, therefore, not well adapted for the purpose intended and the results obtained, as interpreted by Plateau, are misleading.

In another series of experiments, Plateau unsuccessfully attempted to draw insects to flowers by means of the odoriferous essences of lavender, thyme, sage, and mint. "The Labiatae are habitually much visited by bees and I hoped in giving the preference to essences extracted from these plants to see bees and allied insects drawn to the flowers." Essences of orange and bergamot were also employed. But the attraction proved very small or non-existent. Certain essences as thyme and sage were feebly attractive, while mint was even repellent.[14]

Knuth makes the following comment: "From these experiments it follows that solutions of odoriferous plant extracts, which ought to attract insects, do not do so."[15] Plateau subsequently attributed the failure of the flowers to attract insects to the too violent and medicinal odors of the extracts employed; they never possessed the delicate perfume of the plants from which they were extracted. In a new series of experiments undertaken in the spring and summer months of the years 1907-9, instead of odoriferous essences, odoriferous liquid foods, which it had been previously ascertained were attractive to insects, were introduced into neglected flowers. The sweet liquids employed were anisette[16] (essence of anise, syrup of sugar and diluted alcohol), the cooked juice of cherries, syrup of cassonade[17] (syrup of brown sugar to which a few drops of rum had been added), and syrup of Angelica[18] (syrup of cane sugar flavored with a strong aromatic essence obtained from the petioles of *Angelica officinalis*). Fifty-five experiments were performed with these syrups, but descriptions of only a part of them were published, those being selected which most strongly sustained his views, while a few particulars were given in regard to his other experiences.[19]

---

[14] Plateau, F., "Comment les fleurs attirent les insectes," 5me part., *Bull. de l'Acad. roy. de Belgique*, **34**:872–5, 1897.

[15] Knuth, P., "Handbook of Flower Pollination," **1**:207.

[16] A bee-keeper in California reported that he found essence of anise very useful in attracting swarms of bees to empty hives, while another bee-keeper in Ohio did not find it of much value. Gleanings in Bee Culture, **40**:482.

[17] This is somewhat similar to the mixture used in "sugaring" for moths. *Psyche*, **19**:195.

[18] The tender stalks are preserved in sugar and sold as a confectionery.

There will be described in the present paper a few of the more interesting experiments performed by Plateau on relatively large and brilliantly colored flowers seldom visited by insects, following which will be given the observations of the writer on similar flowers. Among the familiar species selected by Plateau was a purple-flowered variety of *Clematis Jackmanni* Jack., a hardy perennial vine widely cultivated both in Europe and America. The flowers are nectarless, but bees obtain from them a small amount of pollen. A vine of *C. Jackmanni superba* is described by Plateau as covering a wall three meters in height and displaying many hundred magnificent blue-violet flowers, which are said to have been wholly ignored by insects. On a very warm clear day anisette was introduced into eleven flowers, near each other, and constituting a group by themselves. In the hour following, they were visited by fourteen bumblebees and six flies belonging to the family Syrphidae. In four instances bumblebees examined adjacent flowers which remained in their natural condition.

The facts related by Plateau are not called in question; but it should be noted again that the ungarnished flowers possessed only conspicuousness and pollen, while the eleven flowers containing anisette possessed conspicuousness, pollen, an agreeable odor and a sweet liquid; evidently color was not here brought directly into competition with odor. Let us now endeavor to determine whether the purple flowers are as completely neglected by insects as Plateau supposed; and whether insects can not be induced to visit them in large numbers without the addition of an agreeable odor! The purple-flowered *Clematis* on which my observations were made was a small vine bearing only eleven flowers wholly or partially expanded. The flowers were of large size, pale purple, nectarless, and odorless. As regards brilliancy of coloring and number, they were at a great disadvantage compared with the inflorescence described by Plateau. They were very frequently examined during the entire period of blooming.

---

[19] Plateau, F., "Recherches expérimentales sur les fleurs entomophiles peu visitées par les insectes rendues attractives au moyen de liquides sucrés odorants," *Mem. de l'Acad. roy. de Belgique*, 2me sér., **2**:1–55, 1910.

On June 11, 1912, a warm clear day, a honey-bee was observed at 12:35 p. m., gathering pollen, also a wild bee which flew away so quickly that it could not be determined. The honey-bee visited four or five flowers before returning to the hive. A few minutes later a second and third honey-bee came for pollen; and during the succeeding hour one or two workers were constantly visiting the flowers for this purpose. One of them remained for a long time, and the loads of purple pollen in the pollen-baskets were plainly visible. Two females of *Halictus craterus* came for pollen. A bumblebee inspected the flowers, but did not alight. A small undetermined bee flew from flower to flower apparently looking for pollen. At 1:35 p. m., there were no insects on the flowers; but a little later a small species of *Halictus*, and also a female of the larger *Halictus craterus* arrived and removed all the pollen remaining available. On three other occasions a female *Halictus craterus* was seen collecting pollen, which in one instance colored purple the under side of the abdomen and the brushes on the posterior legs. No attempt was made to capture any of the bees since this would have lessened the normal number of visits.

The nectarless flowers of *Clematis* were not, therefore, entirely neglected by insects; but were visited by a number of bees sufficiently large to remove all the pollen they produced, and to have effectively pollinated the stigmas had they been in a normally receptive condition, and as this is all that is required, additional visits would have been of no advantage. The sterility of the flowers is not thus due to the absence of pollen-carriers as Plateau supposed. The flowers should be examined immediately after anthesis before the pollen has been removed; since Plateau makes no mention of the pollen he probably did not observe whether it was removed or not.[20] I inspected the flowers many times without finding any insects, and it is easy to understand how a casual observer might gain the impression that they were entirely neglected. Plateau's failure to discover insects on the flowers in their natural condition may have been partly due to an insufficient number of observations, partly to location, and partly to the absence of suitable species of bees. Bumblebees are not well adapted for gathering the scanty supply of pollen, and probably seldom make the attempt. After the pollen has been entirely removed there is, of course, no reason why bees should continue their visits. In an earlier paper I have shown that flowers frequently visited by bees were almost entirely deserted when the corollas were removed; there is, therefore, good reason to believe that the purple sepals of *Clematis* attract the attention of insects.

---

[20] Cowles has suggested that Plateau failed to see the earlier visits of his insects, Cowles, H. C., " Insects and Flower Colors," *Bot. Gaz.*, **39**:70, 1905.

I next proceeded to place on a few flowers an odorless sweet liquid for the purpose of ascertaining whether they would not be visited by bees in large numbers. White granulated sugar dissolved in equal parts of water yields an odorless and colorless syrup, as is admitted by Plateau.[21] June 16 and 17 were cloudy, rainy days, but the 18th was fair. At 8 o'clock a. m., a small quantity of syrup of sugar was placed on three flowers. No visitors were observed until 9:15, when two females of *Halictus craterus* began feeding on the syrup; five minutes later there was a honey-bee at the syrup and a female of *Halictus craterus* gathering pollen. Sugar syrup was now placed on a fourth flower. At 10:00 o'clock there were three honey-bees and one female *H. craterus* feeding on the syrup, a second female *H. craterus* on a flower without syrup, and a third hovering in the air. Ten minutes later a honey-bee left a flower on which there was syrup and flew to two empty flowers; but, after carefully examining their centers and finding nothing, it returned to the flower on which it had previously been at work. The bees were compelled to learn by experience which flowers contained syrup and which did not. I replenished the supply of syrup from time to time as it was consumed, and at 12:15 p. m., there were seven honey-bees sucking on the flowers. On the morning of June 19 I again put syrup of sugar on the flowers, and presently three or four bees were at work. It seemed needless to continue the experiment further, for the bees came from my apiary and it was only a question of time and of supplying the syrup in sufficient quantity to have attracted them in great numbers. During the latter part of this experiment there were eighteen flowers in bloom. Plateau's assumption that the flowers would not be visited unless they were given an agreeable odor was shown to be wholly erroneous; the addition of an odorless sweet liquid secured the visits of insects in far greater numbers than were observed by him.

---

[21] Plateau, F., " Recherches expérimentales," etc., p. 19.

Another common flower selected by Plateau for experiment was the edible garden pea, *Pisum sativum* L. The flowers are rarely pollinated by insects, and self-fertilization is almost invariable. It was for this reason selected by Mendel for his celebrated experiments in hybridization. He says: "Among more than 10,000 plants which were carefully examined there were very few cases where an indubitable false impregnation had occurred."[22] During four summers, however, Müller frequently saw the flowers visited by both sexes of *Megachile pyrina*, and the females both sucked nectar and collected pollen.[23] Plateau's observations were confined to walking on two occasions through many cultivated fields of peas, in one of which he saw a single *Bombus agrorum.*

Plateau introduced anisette into a dozen, or, on one day, two dozen flowers of *Pisum sativum* growing in his garden, which were carefully observed for from one to three hours on five days. The anisette was renewed each day. Twenty visits were made by species of *Bombus* and *Megachile*; and ten visits by flies and small bees which could not possibly effect pollination. Plateau attributed the small number of insects attracted by the odoriferous liquid food to frequent interruptions by rain.

The flowers of the common garden pea are rarely visited by insects, not because they are nearly odorless and the coloration is of no value, but because of the difficulty of depressing the carina. This species no longer exists in the wild state; and, according to De Candolle, was probably introduced into Europe from Western Asia.[24] Müller says: " In its original home the pea no doubt adapted itself to some strong and at the same time diligent and skillful species of bee, which could easily depress the carina, and was plentiful enough in ordinary weather to act as the regular fertilizing agent. Under such conditions, the advantages of firm closure would outweigh the disadvantages. In our climate the pea fails to find bees adapted to its flowers, and it would be much better for it under these altered conditions to have its flowers less firmly shut."[25]

During the summer of 1912, I saw the flowers of the garden pea visited a few times by females of *Bombus fervidus* only; but in other seasons I have occasionally observed honey-bees endeavoring to find nectar in the flowers. The visits of the bumblebees were made in the legitimate way, but I was unable to approach near enough to determine whether the carina was actually depressed or not. In each instance, the bee visited only three or four flowers, probably because it experienced difficulty in obtaining the nectar which was not abundant.

---

[22] Bateson, W., " Mendel's Principles of Heredity," p. 342. Bateson is of the opinion that Thrips may be a source of error.

[23] Müller, H., " Fertilization of Flowers," p. 214.

[24] De Candolle, A., " Origin of Cultivated Plants," p. 329.

[25] " Fertilization of Flowers," p. 214.

In this connection, it is a matter of surprise that Plateau passes over the flowers of the sweet pea, *Lathyrus odoratus* L., without mention. This species belongs to the same family as the garden pea, to which it is closely allied in form and structure, though differing in details. Although the blossoms have a strong and pleasant odor suggestive of honey in addition to the most brilliant hues, it is yet more sparingly visited by insects than the garden pea. According to Plateau, the nearly scentless flowers of the garden pea require an agreeable odor to attract insects; but the fragrance of the sweet pea, which is so pleasing that any effort to improve it would be as futile as the proverbial attempt to paint the lily, does not give the inflorescence any permanent advantage over that of the garden pea. If the absence of insects from the garden pea shows that the influence of its coloration is of no significance, then it may be inquired does not the absence of insects from the sweet pea prove that both color and odor are of no importance? Bees neglect to visit the sweet pea frequently not because these two allurements are of no benefit, but because they have learned from experience that they can not obtain nectar. To attract numerous visits, both the garden pea and the sweet pea require an available food supply.

Place a honey-bee on one of the wings of the sweet pea, and it is at once apparent that it is neither large enough nor strong enough to depress the carina. Repeated examinations of the flowers continued through several weeks of the summer of 1912 failed to reveal a single visit by any species of bee. But by September 22, the autumnal honey-flow from the golden-rods was over, and the honey-bees were at liberty to give more attention to the few other flowers still remaining in bloom. On this date I repeatedly saw honey-bees alight and examine the flowers of the sweet pea, but they made no attempt to depress the keel. One probed diligently between a wing petal and the keel, while another sought for nectar under the calyx lobes, at one time standing on the back of the standard. None of their efforts proved effectual.

Neither can any of our Maine bumblebees depress the carina. On September 26 I saw a female *Bombus fervidus* visit illegitimately twenty flowers in succession. Standing sideways on the flower, clinging to one of the wings and the calyx, she inserted her tongue in a crevice between the standard and a wing petal. Subsequently she robbed many other flowers of their nectar in the same way. The nectar was also obtained in a similar manner by a worker of *Bombus consimilis.**

Until the summer of 1912 I did not suppose that any of our indigenous bees could properly pollinate the flowers; but on August 17 and September 15 and 22, a female leaf-cutting bee, *Megachile latimanus*, was observed to visit the flowers legitimately. She manifested so little fear that I was able to watch her movements at close range. The stigma protruded for a long distance, touching the abdominal scopa on one side and on the other the brush of hairs on the tibia of the posterior leg. Both brushes were thickly covered with pollen. In England, also, according to Punnett, a species of *Megachile* is able to depress the carina.[26] Müller saw only *Anthidium manicatum* sucking on the flowers.

Neither color alone in the garden pea nor color and odor combined in the sweet pea will induce frequent visits, if nothing is to be gained thereby; but, if an odorless sweet syrup is placed on the flowers, bees will resort to them in large numbers. On the morning of August 16 I placed syrup of sugar on a number of sweet pea blossoms. Three times during the afternoon I found a worker of *Bombus consimilis* feeding on the syrup—probably the same bee in each instance. On the 17th I renewed the supply of syrup, and at about 12:30 p. m., a honey-bee discovered it; an hour later there was three honey-bees. Before the close of the afternoon, four honey-bees and two bumblebees were sucking the syrup, or flying about the flowers to which it adhered in small drops. It is evident that they must have occasionally inspected the blossoms, or they would not have discovered the colorless and odorless liquid. By frequently replenishing the syrup, an indefinite number of bees might have been attracted. There was sugar syrup on about ten flower clusters. An available and abundant food supply is required, therefore, to secure numerous and continued visits.

**Bombus consimilis* Cr. is doubtless correctly regarded as a synonym of *B. vagans* Sm., but as the local specimens agree exactly with a set of the three forms of *B. consimilis* obtained from the Ac. Nat. Sci. Phil. the name has been permitted to stand in this paper.

[26] Punnett, R. C., " Mendelism," p. 188.

Let us now inquire whether similar results can not be obtained in the case of the garden pea, *Pisum sativum.* On a clear and moderately warm morning (July 31, 1913), at 8:00 o'clock, about forty flowers of this species were dipped in sugar syrup, a few, small drops of the thin, colorless and odorless solution adhering to each corolla. The garden was in a secluded location, which had not been planted previously for many years, and was nearly surrounded on two sides by a tall cedar hedge. During the half hour following, a honey-bee inspected the flowers on another row of peas, but failed to find the flowers garnished with sugar syrup. At 8:40 a. m., a white-banded wasp, *Vespa consobrina* Sauss, was also seen examining the flowers on another row of peas, and presently, more fortunate than the bee, it came to the flowers on which there was sugar syrup. For the larger part of the day this wasp, and a little later a second wasp of the same species, worked diligently gathering the sweet liquid. I recorded many of their visits, but it would be tedious to relate them in detail.

At 9:10 a. m., a honey-bee was observed inspecting ungarnished flowers of the garden pea; it alighted on the carina and then sought unsuccessfully to reach the nectar through the side of the flower. Ten minutes later a honey-bee discovered the flowers with syrup, and subsequently it continued to return to them at intervals until 10:20 a. m., when I closed the experiment. It met with many disappointments as it often examined ungarnished flowers. The pea blossoms were also visited by a yellow-banded wasp, *Vespa germanica* Fab. At 4:00 p. m., I found both species of *Vespa* still resorting to the flowers.

On August 2, a hot, clear day, at 12:30 p. m., forty flowers of the garden pea were supplied with sugar syrup, which was almost immediately found by a honey-bee and a *Vespa consobrina.* At 12:45, a second honey-bee and a *Vespa germanica* came to the flowers. In another part of the garden a female *Megachile melanophaca* (one of the larger leaf-cutting bees), was observed to visit ungarnished flowers in the normal way. At 1:15 o'clock there were two honey-bees, two *Vespa consobrina* and the small pale blue butterfly, *Lycaena pseudargiolus*, sucking syrup from the flowers; and fifteen minutes later one honey-bee, two *V. consobrina* and two *V. germanica*. The visits continued until 2:45 p. m., when I closed the experiment.

The number of visits by bees and wasps received by the flowers of the garden pea garnished with sugar syrup, during the time they were under observation, was much greater than I had expected. Under the conditions I should not have been surprised had there been no visits by Hymenoptera. On the night preceding August 2 there had been much rain, and the following morning was very foggy, so that the leaves of the pea vines at noon were covered with small drops of water, which could not be distinguished from drops of sugar syrup. The bees made many fruitless visits to flowers without syrup and also to flowers on the wrong row. But both bees and wasps soon learned to confine their attention chiefly to the end of the row with garnished flowers.

There were many small Syrphid flies, as well as larger flies, flitting about among the foliage of the pea vines. Although they not infrequently came to the flowers on which there was sugar syrup, but little importance was attached to their visits, as evidently they might be largely the result of chance. One or two smaller bees belonging to the genera *Sphecodes* and *Prosopis* were also among the visitors. But the larger aculeate Hymenoptera, whose visits are manifestly purposive, were regarded as much better adapted for observation than small, little specialized insects. It was conclusively shown that an available food supply, without the addition of an agreeable odor, would induce numerous visits of honey-bees and social wasps to the odorless flowers of *Pisum sativum*.

" The many horticultural varieties, known under the name of *Petunia hybrida* and cultivated in all gardens, have resulted, as is well understood, from crossings between *P. nyctaginiflora* Juss. and *P. violacea* Lindl. They offer this very interesting peculiarity, from the point of view of the present work, of receiving no visits from the domestic bee, notwithstanding the brilliancy and dimensions of their beautiful, infundibuliform, white, rose, violet, or purple flowers."[27] Plateau, however, observed visits by many bumblebees, and species of Diptera belonging to the genera *Eristalis* and *Syrphus*.

Plateau employed in his first experience a large group of Petunias, surrounded by other plants, as *Tagetes patula* and *Scabiosa atropurpurea*, attractive to bumblebees, flies and butterflies; while among the Petunias there was a single stalk of *Borago officinalis* which alone was visited by honey-bees. On a clear but cool August morning, at 9:30 o'clock, he introduced the odoriferous juice of cooked cherries into six flowers near the stalk of borage. At 3:30 p. m., of the same day, the honey-bees discovered the cherry juice and entirely abandoned the borage flowers for the Petunias. During an hour there were fourteen arrivals, each individual visiting many of the garnished flowers, and rarely a few of the empty flowers. Essentially similar results were obtained in Plateau's other observations on Petunias.

The two common species of *Petunia* endemic to South America have long narrow tubes, are strongly scented in the evening, and are either adapted to crepuscular Lepidoptera or are ornithophilous; in either case we should not expect to find honey-bees among their legitimate pollinators. The hybrid forms of cultivation, moreover, are destitute of nectar; and even if it were present the throat of the corolla is so obstructed by the filaments and style that it would be inaccessible to them. Plateau asserted that an odoriferous syrup was required to attract visits by honey-bees, but it can readily be shown that the presence of an odorless, sweet liquid will render their visits very numerous. A medium sized group of single-flowered Petunias of various colors was selected for my observations.

On July 31, 1913, there were only two flowers in bloom, into both of which I introduced sugar syrup. A bumblebee inspected both flowers but overlooked the syrup. On the 2nd there were two fully expanded flowers, and one which had wilted and closed. A honey-bee examined all three, and remained a long time in one of the open flowers. As the sugar syrup had evaporated, the supply was renewed. The honey-bee returned and thirty minutes later was still visiting the flowers. On the following day a female *Bombus consimilis* was a visitor.

---

[27] Plateau, F., "Recherches expérimentales, etc." *Mem. de l'Acad. roy. de Belgique*, 2me sér., 2:46, 1910.

On August 10, I introduced sugar syrup into nearly all the expanded flowers. *Vespa consobrina* was a constant visitor throughout the day, and subsequently *Vespa germanica* was also observed on the inflorescence.[28] At 2:30 p. m., a honey-bee appeared and continued its visits for half an hour. The day following was very cold and windy for mid-summer; but the 12th was clear and warm. At 9:05 a. m., I introduced sugar syrup into the expanded flowers. A honey-bee was soon at work, and by 11:00 o'clock the number had increased to three; at 12:45, there were four honey-bees and a *V. consobrina*; at 2:35 there were five honey-bees and a *V. consobrina*; and at 6:00 p. m., the wasp and six honey-bees. The number of flowers in bloom was about thirty-five. The weather continued fair on the 13th, and in the morning I found four honey-bees on the flowers. A new supply of sugar syrup was provided, and by 9:10 a. m., there were twelve honey-bees at work. Manifestly, it was needless to continue the experiment further. Thus, without the addition of an agreeable odor, but merely by introducing a supply of an odorless, colorless syrup the visits of honey-bees were induced in great numbers.

Although sugar syrup was not again introduced into the flowers, on August 14, 15 and 16 I saw honey-bees examining the inflorescence, doubtless remembering their former experience. On September 2, a honey-bee alighted on two flowers and examined others; by this time most, if not all, of the flowers into which syrup had been introduced had wilted. Bumblebees were also seen to visit the flowers occasionally, but not finding nectar, they did not remain long. There were many small Diptera flying about the foliage of the Petunias, but little or no significance was attached to their visits. A small bee of the genus *Halictus* also alighted on the corollas.

Pelargonium zonale Willd., says Plateau, is one of the more noteworthy forms of plants with very brilliant flowers, which are almost wholly ignored by insects; the beds of scarlet Pelargoniums, commonly called red geraniums, of which there are a profusion in public gardens, permit us to establish this fact each year. A large bed of *Pelargonium zonale* displayed more than fifty umbels of scarlet flowers; into three umbels on the left side of the bed Plateau introduced the cooked juice of cherries, and in two umbels on the right side anisette was used. Immediately many flies belonging to the families Muscidae and Sarcophagidae, and later two Syrphidae and three wasps were attracted to the odoriferous liquids. The clusters which remained in their natural state are said not to have received a single visit.

---

[28] For the determination of the specific names of these wasps I am indebted to Mr. S. A. Rohwer.

A large plant of *Pelargonium zonale*, of the variety called " General Grant," produced in my garden during the larger part of the summer of 1912 numerous bright scarlet umbels. The nectaries had disappeared and the stamens were largely petaloid so that the flowers yielded neither nectar nor pollen; notwithstanding frequent inspections no insect visits were observed during the larger part of the season. On September 23, at 1:00 p. m., odorless sugar syrup was introduced into two umbels near the center of the plant. From the 23rd to the 26th, no insects found the syrup, which was renewed from time to time as it evaporated. The 26th was warm and clear, and in the afternoon I saw a honey-bee inspect a cluster of flowers near the ground, but it did not alight. The weather continued fair on the 27th, and at 7:00 a. m., there were no insects on the flowers; but at 9:00 o'clock there were, at least, a dozen honey-bees feeding on the syrup, which was speedily consumed. There were six other fully expanded umbels on which there was no syrup, and it was interesting to note how the bees searched them again and again in their efforts to find more of the edible liquid. Two other umbels with a few buds partially open were also carefully examined. Their attention at first was entirely confined to the gaudy flowers, but later they discovered some of the liquid, which had dripped on a few leaves, and removed it. Their number continued to increase so long as I supplied the syrup. Later they flew to a bed of *Portulaca grandiflora* Lindl., to the inflorescence of which they had never before been seen to pay any attention, and inspected flower after flower but seldom alighted.[29]

Evidently the bees had learned from past experience to associate the presence of nectar with conspicuousness, and though they had never found any food in these particular flowers, they had no doubt continued to occasionally inspect them, as in the single instance observed on the 26th, when a bee inspected an empty umbel but failed to visit those containing syrup. After they had found syrup on two of the umbels, they examined all the others very thoroughly, and also other flowers in the garden previously neglected. They discovered the syrup on the flowers long before they did that which had dripped on a few leaves, and the discovery of the latter was incidental to their visits to the flowers. The bright coloration was clearly an advantage in this instance in enabling honey-bees in large numbers to find the odorless sweet syrup. Obviously highly specialized bees are much better adapted for the purpose of such an experiment than the common flesh-flies observed by Plateau.

---

[29] During a part of the time this experiment was in progress one of the colonies in my apiary was allowed to remove the honey from a few partially filled combs; and it subsequently occurred to me that this probably stimulated the bees to search the flowers more diligently for nectar.

Plateau made many additional experiments in the course of which he introduced odoriferous syrups into the flowers of *Lilium candidum* L., *Passiflora adenophylla* Masters, *Œnothera speciosa* Nuttal, *Linum perenne* L., and *Convolvulus sepium* L., with the result that insects in variety were attracted. But it is unnecessary to consider his experiences further since insects in large numbers may also be attracted to conspicuous, neglected flowers by means of an odorless sweet liquid. Since Plateau knew that sugar syrup was odorless it is natural to inquire why he failed to employ it in control experiments. On four occasions he did introduce syrup of sugar into the flowers of *Lilium candidum*, in three instances into two flowers and in one instance into six flowers. He says that, as he foresaw, syrup of sugar without odor did not show any power of attraction.[30] But a small number of Diptera, as *Syritta pipiens*, *Melanophora roralis*, *Anthomyia radicum* and *Calliphora erythrocephala*, did find the syrup and profit by their discovery. No information is given as to the length of time the flowers were under observation. The number of visits received, however, was about the same as in the case of *Polygonum Convolvulus*, when anisette was added to eight groups of flowers on a very warm clear day. Certainly the list of Diptera recorded gave promise that many visits would have been received had the supply of syrup been continued for a longer period. *Lilium candidum* is a campanulate flower two or three inches long adapted to pollination by hawk-moths, and it is easy to understand that some time might elapse before the deeply concealed syrup was found by Hymenoptera. No mention is made of the use of sugar syrup in any other control experiments, an omission which can hardly be regarded as excusable.

---

[30] "Recherches expérimentales sur les fleurs entomophiles," etc., p. 19.

It seems desirable, therefore, in this connection to give a few additional instances observed by myself, where the introduction of sugar syrup resulted in frequent visits of bees. A group of *Zinnia elegans* Jacq., in my garden, was almost wholly neglected by insects. On the morning of August 16, I introduced syrup of sugar into several capitula, renewing the supply the following day. During the forenoon of the 17th, a honey-bee examined the ray flowers of two ungarnished capitula, and then, coming to a head, containing syrup, sucked for a short time. Later a worker of *Bombus consimilis* found the syrup. At 12:30 p. m., there were on the flowers two honey-bees and two worker bumblebees, *Bombus consimilis* and *B. terricola*. At 3:30 p. m., there were seven honey-bees and one bumblebee on the flowers—there was syrup in a dozen capitula. The honey-bees also examined the capitula which remained in their natural condition. The experiment was now discontinued. Three days later, on August 20, a honey-bee, undoubtedly one of the former visitors, examined many capitula; evidently it remembered its previous experience.

The brilliantly colored flowers of the scarlet runner, *Phaseolus multiflorus* Willd. var. *coccineus* Lam., contain nectar; but owing to the difficulty of depressing the carina, are much neglected by insects. Occasionally in this locality females of *Bombus fervidus* visit the flowers legitimately. I have also seen a honey-bee for several hours fly from flower to flower inserting its tongue in the opening beneath the standard, and apparently able to reach a very small quantity of the nectar. On the morning of August 16, I put sugar syrup on a few corollas, and during the afternoon there were always from four to six bees on the flowers. They also inspected flowers on which there was no syrup. On the 17th, I renewed the supply of syrup and the bees continued their visits during the entire day.

Honey-bees have not sufficient strength to depress the carina and obtain the nectar normally; but if the nectaries are punctured they will then visit the flowers in great numbers. Every year the scarlet runner is under cultivation in my garden, but I have never known bumblebees to bite holes in the flowers except in 1908. On August 14 of that year, the vines were in full bloom, and there were present many workers of *Bombus terricola*, which perforated the flowers as fast as they matured—so far as I could discover not a single blossom escaped. The holes were all on the under side of the calyx on the left hand side, which may be explained by the fact (also observed by Müller[31]) that the more powerful bees almost invariably alight on the left ala. The honey-bees promptly discovered the holes and used them most diligently for extracting the nectar. There was no pretence on the part of either honey-bees or bumblebees of making normal visits. The absence of bees from the flowers of the scarlet runner does not, therefore, prove that their brilliant hue is of no advantage, or that an agreeable odor is required, for it is only necessary to render the nectar easily accessible by punctures to induce the visits of bumblebees and honey-bees in great numbers.

The correlation existing between the accessibility of nectar and the number of honey-bees present is also most instructively shown by the inflorescence of red clover, *Trifolium pratense* L. The flowers are pollinated chiefly by bumblebees, which are frequent visitors, and in their absence are largely sterile. An historical illustration is the well-known experience of the agriculturists of New Zealand, in which country at the time of its discovery there were neither honey-bees nor bumblebees. In consequence the yield of seed did not become commercially profitable until in 1855, when about one hundred bumblebees were imported from Europe.[32]

The nectar of red clover is secreted at the base of a tube a little over 9 mm. in length, where it is beyond the reach of the tongue of the honey-bee. This has occasioned much regret among bee-keepers, for the flowers not only secrete nectar very freely but the quantity is not greatly affected by weather conditions. Repeated attempts have been made to develop a strain of red clover bees, but the gain in tongue length has invariably proved only temporary. Under normal conditions, then, honey-bees do not frequently resort to the red clover fields; but occasionally in very dry weather the floral tubes become so short that large yields of honey are obtained. Two or three times during the last thirty years at Borodino, N. Y., red clover has been a very valuable source of honey; and one season fully sixty pounds, on an average, to a colony was secured.[33] An apiarist in Michigan reports that in one year his bees stored 500 pounds of pure red clover honey as surplus.[34] The black bees stored none, the hybrids only a little, while the bulk of the 500 pounds was gathered by Italian bees. The length of the tongue of the common black bee is 6 mm., of the pure Italians, not over 7 mm., while that of the hybrids is intermediate. Thus there was presented the singular spectacle of fields of red clover visited by thousands of Italian bees, while the black bees were absent. Had the drought shortened the corolla tubes another millimeter the nectar would have been accessible to black bees, and they, too, would have been present.

---

[31] Müller, H., "Fertilization of Flowers," p. 216. Both honey-bees and bumblebees almost invariably alight on the left ala. The reason for this is that the spirally coiled carina closes the entrance beneath the standard on the right hand side. Usually the alae stand apart, but when one occasionally overlaps the other, honey-bees alight on the center. Bumblebees visit the flowers of the common, garden bush beans in a similar manner.

[32] Knuth, P., "Handbook of Flower Pollination," translated by J. R. Ainsworth Davis, **2**:292. Jarvis, P. D., "Bumblebees that Fertilize Red Clover," *Rep. Ent. Soc. Ont.*, **36**:128. Graenicher, S., "New Zealand's Experience with the Red Clover and Bumblebees," *Bull. Wis. Nat. Hist. Soc.*, **8**:166.

But undoubtedly the most remarkable illustration ever recorded of the relation of rainfall to the length of the corolla-tubes, and consequently of the accessibility of the nectar to honey-bees, was observed by an apiarist at Medina, Ohio. Of two apiaries belonging to him one is located near Medina, and the other two miles north of that city. A few years ago (1906) there was a drouth at the north bee-yard, and the floral tubes of the red clover were so much shorter than usual that honey-bees were able to reach the nectar. When one of the farmers began to cut his field of red clover that season, the cutter knives of the mower stirred up so many bees that they attacked the horses and their driver. So numerous and pugnacious were they that it looked as though they would prevent anyone from cutting off their supply of honey.

Singularly enough at Medina and the south bee-yard, there was an abundance of rain. Here, when he went over a big field covered with a luxuriant growth of red clover scarcely a bee could be found. The corolla-tubes were so long that the bees could not obtain the nectar, and consequently, there were none on the clover heads. Thus two bee-keepers, living only a few miles apart, might have arrived at diametrically opposite conclusions as to the value of red clover as a honey plant.[35]

---

[33] Doolittle, G. M., " Honey from Red Clover," *Gleanings in Bee Culture,* **34**:993.

[34] Hutchinson, W. Z., " Red Clover," *The Bee-Keepers' Review,* **21**:342.

It is clear that the presence or absence of honey-bees in large numbers on the flowers of red clover is not determined by the color or odor, but by the accessibility or inaccessibility of the nectar. Drouth may not render the nectar accessible more than once in ten years, but when it does happen, the bees promptly avail themselves of the opportunity. Evidently they must inspect the flowers each season, but, finding no booty, they do not often repeat their visits. The utter inconsistency with the facts of the claim that the absence of insects from certain conspicuous flowers proves that bright coloration is of no advantage and that an agreeable odor is a necessity, could not be better shown than in the instance where the Italian bees were able to obtain the nectar and the black bees were not.

The flowers of alfalfa, *Medicago sativa* L., a leguminous plant very extensively cultivated in the west for forage, offers very similar phenomena. In the irrigated regions of California and Colorado, nectar is yielded so abundantly that alfalfa surpasses all the other local honey plants in importance, even the famous purple, black and white sages of the former state. But in Kansas, for example, the results are strikingly different. In the Western part of the state along the river bottoms the flowers can usually be depended on for nectar during most of the season, while around Topeka, bees only occasionally visit the bloom. A bee-keeper who has lived in Eastern Kansas for thirty-five years states he has never seen a bee on the flowers, or known of a pound of alfalfa honey being produced in that section.[36] Where alfalfa, then, secretes nectar freely the vast acreage is constantly the resort of millions of bees; but in localities where it is nectarless, their visits are so rare that the flowers appear to be entirely deserted through a long series of years. Honey-bees do not usually visit the flowers legitimately, but procure the nectar through a crevice in the side.

---

[35] Root, E. R., " Red Clover as a Honey Plant," *Gleanings in Bee Culture*, **34**: 990. The three apiarists cited in this article are careful observers and recognized authorities on bee-culture. Buttel-Reepen has remarked: " It seems to me that the biological knowledge concerning *Apis mellifica* which has been gained by practical bee-keeping has scarcely entered scientific literature . . . In proof of this there are the vague, defective assertions which are found in the newest editions of scientific works." "Are Bees Reflex Machines," p. 1.

[36] Root, E. R., " Bee-keeping in the Semi-arid Regions of Oklahoma, Kansas and Nebraska," **41**:345. In the eastern states of North America, white clover, *Trifolium repens* L., is the foremost honey plant, and the domestic bee stores from its bloom annually hundreds of tons of an excellent, white honey; but in France and Switzerland it yields no appreciable quantity of nectar and one may travel several kilometers and not see a bee on it. " White Clover in Europe," *Am. Bee Journal*, **53**:331.

An excellent illustration on a scale of great magnitude showing that honey-bees are guided by the memory of past experience in gathering nectar is furnished by the honey-flow of buckwheat, *Fagopyrum esculentum* Moench., which Buttel-Reepen describes as follows:

" If colonies stand in buckwheat, the flight is lively in the mornings until ten o'clock; then it lessens, and is entirely quiet for the greater part of the day, beginning vigorously again the next morning. The buckwheat nectar flows only in early morning; so, as the nectaries dry up, the bees fly out a couple of times and then discontinue their vain flight. In spite of the shimmering sea of flowers, *in spite of the strong fragrance,* only a few bees may usually be found after ten o'clock in the buckwheat field." [37]

The period of time during which the flowers of buckwheat secrete nectar varies in different localities. In this region the bees continue to work on them, according to observations made by a young friend of the writer, until about 12:30 p. m. Their visits then quickly decrease in number until about 1:00 o'clock, when they cease entirely. But for an hour or more afterwards, the bees may be seen occasionally flying from blossom to blossom, pausing, however, for only an instant, as they apparently discover at once that the flowers are now nectarless. At Delanson, N. Y., buckwheat yields nectar most abundantly between 9:00 o'clock in the morning and 2:00 p. m. A bee is seldom at work on it much earlier or much later, notwithstanding there are hundreds of colonies of bees in the vicinity. In parts of the west, buckwheat is a more uncertain honey plant than in the east and in some years the flowers fail to become nectariferous, when they are almost wholly deserted by bees.[38] Again a sudden shower followed by a fall in temperature may bring the buckwheat harvest to an abrupt and premature close in August, when ordinarily it would continue into September. Such an interruption of the honey season occurred at Delanson in 1906. For several days a hive on scales had shown a gain of eight pounds a day; but during the night of August 24 there was a light shower and a decline in temperature of 11 degrees F., after which the hive on scales did not show a gain of half a pound any day that fall. The bees immediately ceased visiting the flowers, and in countless thousands attempted to rob each other and the honey house.[39] Owing to the intermittent nature of the flow of nectar, bees are more irritable during the buckwheat harvest than during that of any other plant. The time of the flight of the bees thus always coincides with the period of active secretion of nectar, or if the flowers are nectarless they neglect them almost entirely.

---

[37] Buttel-Reepen, H. V., "Are Bees Reflex Machines ? " translated by Mary H. Geisler, p. 29.

[38] Root, A. I. and E. R., " The A B C and X Y Z of Bee Culture," p. 71.

The preceding experiments and studies of honey plants show that honey-bees learn from observation and are guided by the memory of past experience. Flowers rich in accessible food supplies receive numerous visits, but if for any reason the flow of nectar suddenly ceases the bees immediately discontinue their visits. If the inflorescence of a plant species yields abundant nectar in one locality but is devoid of nectar in another, even though only a few miles intervene, the flowers in the former place will be frequently visited and in the latter deserted. But honey-bees do occasionally visit and examine conspicuous flowers from which they can not obtain food materials, and it is upon this premise that the argument of the present paper is based. *A priori* reasoning alone would lead the floroecologist, who believes that conspicuousness is an advantage to flowers to this conclusion, thus Campbell remarks that " it is safe to say that no showy flower is entirely destitute of insect visitors."[40] Much evidence has already been adduced in support of this statement, but it is desirable to give additional observations, made especially for this purpose. The casual observer will often fail to discover a single visitor, and may easily conclude that they never attract the attention of insects; but long continued investigation proves this to be a mistake.

The variegated flowers of the Sweet William, or bunch pink, (*Dianthus barbatus* L.), display the most vivid shades of crimson and scarlet; and, as the name indicates, exhale a pleasant fragrance. They are adapted to pollination by butterflies and day-flying moths. The nectar, while not abundant, is sufficient in quantity to yield a sweet taste to the tip of the tongue; and it lies at the bottom of a calycine tube 15 mm. long, far beyond the reach of honey-bees. Previous to July 11, 1912, I failed to record a single bee visitor. On this date I saw a honey-bee inspect several clusters of flowers, but it never actually alighted, although flying close to the inflorescence. On the 23rd, a honey-bee visited a few flowers. At about 11:00 a. m., August 6, a warm clear day, two and at one time three honey-bees were observed on the flowers. They were carefully watched for ten minutes, and one of them vainly endeavored, standing in various positions; to reach the nectar by thrusting its tongue down the center of the flower. Others probed between the petals, even looking under the corolla. An hour later, a bee was still found on the clusters; at intervals, wasps and flies also examined the flowers. Observations extending through the entire season show that the flowers are very far from being wholly neglected by Hymenoptera and Diptera, although a few inspections might readily lead to this belief.

---

[39] Alexander, E. W., " Buckwheat as a Honey Producer," *Gleanings in Bee Culture*, **35**:394.

[40] Campbell, D. H., ' 'Plant Life and Evolution," p. 227.

The flowers of the bee larkspur (*Delphinium elatum* L.), which are normally pollinated by bumblebees, have so long a spur that the nectar is wholly inaccessible to honey-bees. In my garden they are very rarely visited by insects of any kind. On the morning of July 11, a honey-bee after visiting one or two flowers, desisted from its useless efforts. On July 24, in the afternoon, a honey-bee visited several flowers in an unsuccessful attempt to find nectar. It pushed its tongue as far as possible into the mouth of the spur, and also looked for nectar under the upper perianth segment. On August 4, a bee inspected two blue floral leaves, which had fallen from a flower to the green foliage, thus showing that a single detached petal could gain its attention.

On July 16, a large moth poised before several flowers and obtained the nectar without difficulty; in the evening the white center contrasts so strongly with the blue ground color that the attention of crepuscular Lepidoptera might easily be gained.

During the summer of 1910, no insects were seen to visit the flowers of the pansy (*Viola tricolor* L.). By October 1, nearly all the wild and cultivated flowers had perished, but a few pansies still remained in bloom. October 7 was cold and rainy, but the day following was clear, warm and calm, and at 10 a. m., a honey-bee spent more than ten minutes on the pansy flowers searching for nectar. Two Syrphid flies (*Eristalis tenax*) were also flying from flower to flower looking for pollen, but making no attempt to find nectar. On the afternoon of the 10th, a worker of *Bombus consimilis* and a male of *B. fervidus* were examining the flowers for nectar; and on the 11th a worker of *B. consimilis* and a white butterfly. Thus the pansies are not so much neglected as at first appeared probable, but in the absence of more desirable flowers are frequently visited by insects.

On the morning of October 28, 1912, two honey-bees were examining the larger, neutral flowers of *Hydrangea paniculata* Sieb., but they soon learned that they were nectarless and passed over to the smaller, perfect flowers. On July 16, a species of *Megachile* visited two flowers of the climbing honeysuckle (*Lonicera Periclymenum* L.), a hawk-moth flower; but its stay was very brief, as it could not reach the nectar. It then flew to another moth flower (*Œnothera biennis* L.), which was closed. Finding no opportunity to get flower food it returned to the honeysuckle; but meeting with no better success than on its previous visit, it abandoned that part of the garden altogether. In the evening, while the hawk-moths were industriously at work on the honeysuckle flowers, they repeatedly inspected large, red roses blooming on a bush a few feet away. The roses are pollen flowers and devoid of nectar, but the hawk-moths were compelled to learn this fact by direct examination. Another pollen flower is the poppy, but before the anthers dehisc honey-bees may often be seen searching for nectar at the base of the petals. Honey-bees have likewise been observed looking for nectar under the calyx segments of flowers belonging to the Labiatae.

Further examples that honey-bees occasionally examine carefully flowers, which are commonly neglected, might be multiplied indefinitely; but sufficient instances have been given for the purpose of the present paper. It has been shown that such visits are actually made, and that they are infrequent because the bees remember their inability to obtain flower food. Nevertheless, in the aggregate they do waste much time in fruitless visits to a great variety of flowers, which for one reason or another yield no booty; but this loss is reduced to a minimum by their ability to learn from experience. They are able to store up in their brains, as described by Forel, various sense impressions of color, form and spatial position, by which their movements are subsequently guided and which prevent them from indefinitely making useless visits. " It results, therefore, from the unanimous observations of all the connoisseurs that sensation and perception, and association, inference, memory and habit follow in the social insects the same fundamental laws as in the vertebrates and ourselves."[41] But he adds that " the above mentioned faculties are manifested in an extremely feeble form beyond the confines of the instinct-automatism stereotyped in the species."[42]

In closing this paper it is desirable to remind the reader that the visits of bees to flowers are, of course, often influenced by other factors besides the characters of the flowers, as temperature, rainy or foggy weather, the number of insects in the locality, and especially by the blooming period of common plants very rich in nectar. During the honey-flow from the more important honey plants, bees restrict their visits very closely to a single species, and there is no occasion nor would it be for their advantage to pay attention to flowers containing little or no nectar. Plateau himself noticed that when the apricots expanded their flowers, the Hymenoptera abandoned the violets, and he was forced to discontinue his experiments with artificial flowers.[43] During a honey-flow the entire force of field bees of each colony is largely governed by a common impulse, and their attention may be fairly termed obsessional. The hives may then be opened and the honey exposed with scarcely any danger of robbing. Buttel-Reepen tells of a bee-keeper who placed a dish of honey over his strongest colony during the buckwheat honey-flow, and after eight days of good forage the bees had not touched the honey, although it was pure.[44] Manifestly, under these conditions small groups of conspicuous, nectarless flowers, and even those containing nectar, will be likely to be passed over unheeded.

---

[41] Honey-bees will not visit bright-hued pieces of paper or cloth, whether large or small, attached to a line and suspended over a bed of flowers, or crude floral groups painted on large screens or walls, because they are not deceived by these objects, or images, any more than ourselves. Cf. Plateau, F., " Le Macroglosse," *Mem. Soc. ent. de Belgique*, **12**:141–80, 1906.

[42] Forel, August, "Ants and Some Other Insects," translated by William Morton Wheeler, p. 21.

[43] Plateau, F., " Les fleurs artificielles et les insectes," *Mem. de l'Acad. roy. de Belgique*, **1**:24, 1906.

[44] Buttel-Reepen, H. V., "Are Bees Reflex Machines," p. 27.

CONCLUSIONS

Entomophilous flowers are usually characterized by the possession of either bright coloration, or odor, or both, although apparently to some extent the two qualities are mutually exclusive. Both allurements are useful in attracting the attention of insects; but the absence of either conspicuousness, or odor, or both, will not necessarily cause a flower to be neglected if it contains an ample supply of pollen or nectar. But under similar conditions, small, green, odorless flowers, even if rich in nectar, will not be discovered as quickly as nectariferous flowers, which are conspicuous or agreeably scented.[45] On the other hand, the possession of both color and odor will not ensure frequent visits in the absence of available food materials. The experiments afford no evidence that bees visit flowers for the purpose of experiencing an aesthetic pleasure.

Insects, especially bees, occasionally examine the neglected, conspicuous flowers of cultivation; but, obtaining no food materials, or very little, they do not often repeat their visits. Many neglected flowers are pleasantly scented, and the addition of another agreeable odor is neither necessary nor beneficial.

When odoriferous fruit syrups are introduced into conspicuous flowers, commonly neglected, a group of miscellaneous insects, especially Diptera, will be attracted; but the inference that, therefore, color is no advantage and that an agreeable odor is required is fallacious. For the introduction of an odorless syrup into similar flowers will induce insect visits in large numbers; also when flowers, with the nectar inaccessible to honeybees and, consequently, seldom visited by them, have the nectaries artificially punctured, or the floral tubes shortened by drouth, they are then visited by bees in countless thousands without the addition of either an agreeable odor or a sweet liquid. Flowers which in one locality freely secrete nectar and are visited by numerous insects are sometimes in other localities nectarless and almost entirely neglected. Insects, therefore, perceive the colors and forms of neglected flowers, and the rarity of their visits is the result of their memory of the absence of food materials, not because the flowers lack an agreeable odor, which is often not the fact.

---

[45] Lovell, John H., "The Pollination of Green Flowers," *Amer. Nat.*, **46**:83–107, 1912.

The flowers into which Plateau introduced odoriferous sweet liquids were thus artificially converted into distinct physiological varieties. Since flowers possessing conspicuousness, an agreeable odor, and a liquid food were opposed to flowers possessing only conspicuousness, it is clear that color was never directly brought into competition with odor—the latter was invariably given the advantage.

Colors and odors attract the attention of insects, but bees in their visits to flowers, previously examined by them, are guided largely by the memory of past experience; they are able to associate different sense impressions and unconsciously make analogous inferences.

THE HARVARD LABORATORY OF ANIMAL PSYCHOLOGY AND THE FRANKLIN FIELD STATION

ROBERT M. YERKES

With two figures

It is now fifteen years since the Director of the Harvard Psychological Laboratory, Professor Hugo Münsterberg, made a place for experimental work on the psychology of infra-human organisms in his laboratory. In 1899, two rooms in Dane Hall were assigned to students of animal psychology, and under the direction of the writer, three investigations were conducted. To meet the needs of an increasing number of workers, an additional room was made available in 1902.

In December, 1905, the laboratory equipment, together with all experimental work in psychology, was transferred to a newly and specially planned and constructed laboratory in Emerson Hall. Here, five rooms, in addition to the Instructor's office and a large amount of space in an unfinished attic, were available for work with animals. The following account of the facilities afforded for this work is quoted from a description of the Harvard Psychological Laboratory, published in 1906:[1]

" Several rooms are fitted up with special reference to the investigation of the various forms of organic movement, animal behavior and intelligence. As one result of several investigations in animal psychology already pursued here, the laboratory has a considerable number of devices for testing and making statistical studies of the senses and intelligence, methods of learning and emotional reactions of animals.

"Adequate provision is made for the keeping of animals in a large, well-lighted, and well-ventilated corner room. Instead of having aquaria built into the room, an aquarium-table eighteen feet long has been constructed to support movable aquaria of various sizes. Whenever it is desirable for the purposes of an investigation, any of these aquaria may be moved to the research-room of the investigator or to such quarters as the special conditions of the experiment demand.

---

[1] The Harvard Psychol. Studies, vol. 2, p. 35.

" The vivarium-room contains, in addition to provisions for water-inhabiting animals, cages of a variety of forms and sizes. The largest of these cages, six and a half feet high, six feet wide, and four feet deep, may be used for birds, monkeys, or any of the medium-sized mammals. Cages for rabbits, guinea-pigs, and other small animals are arranged in frames which support four double compartments. Similarly, small cages suitable for mice, rats, and other small rodents are in supporting frames which carry four of the double cages, each of which is removable and may be carried to the experimenting-room at the convenience of the experimenter.

" In a large unheated room above the main laboratory are tanks for amphibians and reptiles. These tanks, since they can be kept at a low temperature during the winter, are very convenient and useful for frogs, tortoises, and similar hibernating animals."

Work progressed satisfactorily in these quarters until the spring of 1913, when the introduction of experimental work in Educational Psychology, rendered desirable a redistribution of space. During the summer of 1913, the unfinished fourth floor of Emerson Hall previously referred to was developed, in accordance with plans prepared by the writer, as a laboratory of animal psychology. The floor plan of this new laboratory is presented in the accompanying figure 1.

Ten rooms, in addition to an office for the director of the work, are now at the service of students of animal psychology. Of these rooms, several were especially planned and have been at least partially equipped for definite lines of inquiry. Thus rooms 40 and 41 have been built about the Yerkes and Watson apparatus for the study of the several aspects of vision in animals. Preliminary studies of vision by simpler rough and ready methods are conducted in other rooms of the laboratory, or at the Field Station described below, and the more elaborate apparatus is used only for accurate and thorough-going investigations. By means of our varied visual equipment, it is possible to study color, intensity, size, form, and distance perception with a degree of exactitude which heretofore has been exceptional in connection with studies of animal behavior.

Room 42 is equipped with the Watson circular maze and the

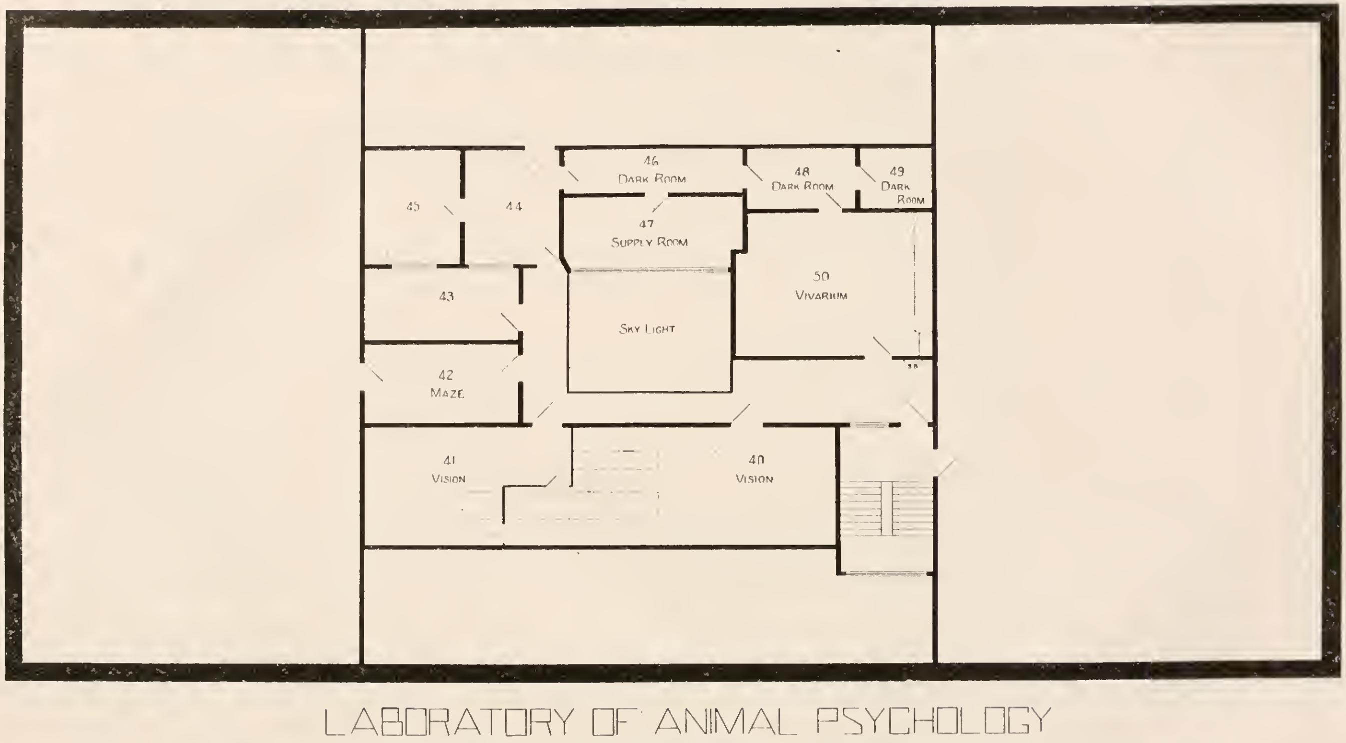

46
Dark Room
48
Dark Room
49
Dark Room
45
44
47
Supply Room
50
Vivarium
43
Sky Light
42
Maze
38
41
Vision
40
Vision
LABORATORY OF ANIMAL PSYCHOLOGY

FIGURE 1. Floor plan of the new Harvard laboratory for the study of animal psychology.

Yerkes and Kellogg graphic record device. The latter enables an observer to obtain accurate records of distance and errors, in addition to those of time, in all maze experiments. Thus, the value of the maze-method is trebled. This improved apparatus demands stability, and, although it may readily enough be moved from room to room, it is eminently desirable to have a suitable place reserved for it, so long as the maze method maintains its present importance and promise as a comparative method and offers so many obvious possibilities of improvement.

The rooms numbered 43, 44 and 45 are daylight rooms as is also 42, which may be employed as occasion demands. At present, two of them are used for studies of problems of heredity in rats and mice. Later, the Hamilton insoluble problem multiple choice apparatus and the Yerkes soluble problem multiple choice apparatus will be installed in this group of rooms. These devices demand a special recorder-room. It is our purpose to install the recorder for both outfits in one room while placing the respective reaction devices in separate rooms. These two sets of multiple choice apparatus will render possible in this laboratory or at the Field Station (since we propose so to construct the apparatus that it shall be readily movable) the study of ideational reactions, in a variety of animal types, in such wise as to furnish directly comparable data of reaction.

The line of dark-rooms numbered 46, 48 and 49, is especially convenient because it may be used either in sections or as a whole. A supply of compressed air is delivered to room 49, and it is intended that in this room, in conjunction with room 48, there shall be installed apparatus demanding air under constant pressure for varied studies of olfaction and audition.

A store room, number 47, provides adequate space for supplies in the shape of food stuffs, bedding or litter, small cages, and packing or transportation boxes. Storage space for larger apparatus and materials is afforded by a room to which entrance is given by the doorway indicated in room 42.

Finally, room 50 is the " animal living room " of the laboratory. The floor of this room is water proof so that cages and aquaria may be thoroughly washed and the floor flushed at need. In this vivarium are set cages for a variety of vertebrates. At present, the laboratory is supplied with cages especially designed for mice, rats, guinea pigs, rabbits, cats, monkeys and birds.

A large aquarium table, upon which any desired form of aquarium may be placed, provides for the housing of amphibians and fishes.

The writer's students' training course in animal psychology is conducted in a class-room and lecture room on the third floor of Emerson Hall. The space of the laboratory on the fourth floor is, therefore, wholly available for research.

The rooms of the new laboratory are supplied with water, gas, compressed air, and a variety of electric currents. The latter are conveniently delivered from boards located in each room. In every room there are available 110 volt direct and alternating currents, as well as currents from Edison storage batteries which are located in the battery room of the main laboratory. A conveniently placed and well constructed switch board (S. B. of Figure 1) in the corridor of the laboratory, provides for the distribution of these storage currents. This board is fitted with miniature Weston switch board voltmeter and ammeter, and with taper plugs.

Realizing the extreme need for apparatus in animal investigations which shall, in a large measure, eliminate the experimenter from the situation to which the animal is expected to respond, the writer, in planning this new laboratory, has attempted so to arrange spaces that automatic setting, actuating and recording devices may readily be placed in rooms adjoining those in which the animal is responding. Heretofore, the majority of students of animal behavior have deemed themselves competent and able to observe and record accurately the doings of their subjects. That this, however, is not the case is clearly proved by numerous instances of misobservation and misinterpretation of reactions. We have, for example, twice discovered in this laboratory that dogs which were presumably responding to a definitely arranged experimental situation were actually responding to certain unconscious movements of the experimenter. The only safe and sure way to avoid such risks is to provide mechanical recorders which shall at least enable the experimenter to separate himself widely from his reacting subject.

We have striven for flexibility and adaptability in this new laboratory of animal psychology while arranging for the development, in designated spaces, of specific forms of apparatus. So far as the conduct of experimental work under highly controllable and reasonably controlled conditions is in question, the laboratory, with its instrumental equipment, is excellent. But in addition to the ever present need of the development of new methods and the opportunity for the advantageous installation of new apparatus, the writer has felt as a still more urgent and important need, the supplementation of the laboratory by facilities for field work.

It would appear to be self-evident, yet the attitude of many experimental students of animal behavior seems to contradict the statement, that every student of animal life should be familiar with the objects of his interest in nature as well as in the laboratory; that he should possess, as a basis for evaluating the results of experiments, intimate knowledge of the instincts, habits, temperaments, and habitat of whatever type of organism he happens to be using for experimental purposes. The writer is fully convinced that naturalistic observation, or field work, should be held alike by naturalists and experimentalists as of equal importance with experimental observation, and should be regarded as an indispensable supplement to the latter. There are naturalists, to be sure, who decry all observation of animal behavior made under experimental conditions, whether within or without the walls of a laboratory, and there are experimentalists who deny the value of naturalistic work, or ignore it. But surely the last decade has furnished abundant proof of the unprofitableness of these attitudes. We propose, so far as is possible, in connection with our laboratory studies of animal behavior, to attempt to unite the naturalistic and the experimental points of view and methods.

The Harvard Psychological Laboratory is particularly fortunate in having the use of a field station in Franklin, New Hampshire, at which naturalistic studies on any organism which will thrive in a temperate climate may be pursued. This station consists of a tract of about one hundred and fifty acres of hill land, of which about half is wooded. The elevation is fourteen to fifteen hundred feet. There are numerous springs and a brook on the tract. Two sets of old farm buildings are available for such needs as arise. This tract, which is constituted by two old farms, was purchased by the writer in the years 1911 and 1912 to serve both as a summer home and as a reservation which might, as seemed desirable, be used for studies in animal behavior

It is proposed that this private field station shall meet two keenly felt needs of the Harvard Laboratory; the one, that of a suitable place for purely naturalistic field work; and the other, that of a similarly suitable place for the conduct of laboratory investigations which cannot well be continued during the summer in Cambridge. We may consider, first, the second of these needs.

There are frequently in progress, in the Harvard Laboratory, researches on heredity or on problems which demand long experimental training, the interruption of which, during the summer vacation, entails serious loss. It is often impracticable to attempt to continue such investigations throughout the summer in Emerson Hall, for even if the investigator is willing to work there, it usually means a serious sacrifice on his part of opportunity for rest and recreation through a change of scenes. The Franklin Field Station, it is hoped, will result in the saving of considerable time to certain investigators, since there it should be possible to continue work uninterruptedly throughout the summer, while at the same time the investigator may profit by the change from city to country and the chance to combine experimental and naturalistic studies in animal behavior with the recreations of a mountainous country.

It is by no means intended that all of the investigations conducted in the Harvard Laboratory shall be transferred to the Field Station. Instead, only a few should or can, to advantage, be so transferred.

But of primary importance, as contrasted with its value as a place for transferred experimental investigations, is the opportunity which the field station offers for naturalistic work. In and about the Cambridge Laboratory, favorable opportunities for training students to observe animals carefully, critically, and at the same time sympathetically, in their native habitats, are rare. And the writer has observed, in many otherwise admirable students of the biological sciences, a tendency toward the acquisition of a narrow minded attitude toward experimental observation, which blinds them to the value of nature-study. It is hoped that at Franklin something may be done for at least a few students of animal behavior to counteract this tendency and to train them to become enthusiastic and reliable naturalists as well as skilled experimentalists.

There is no obvious reason why, at the Field Station, any one

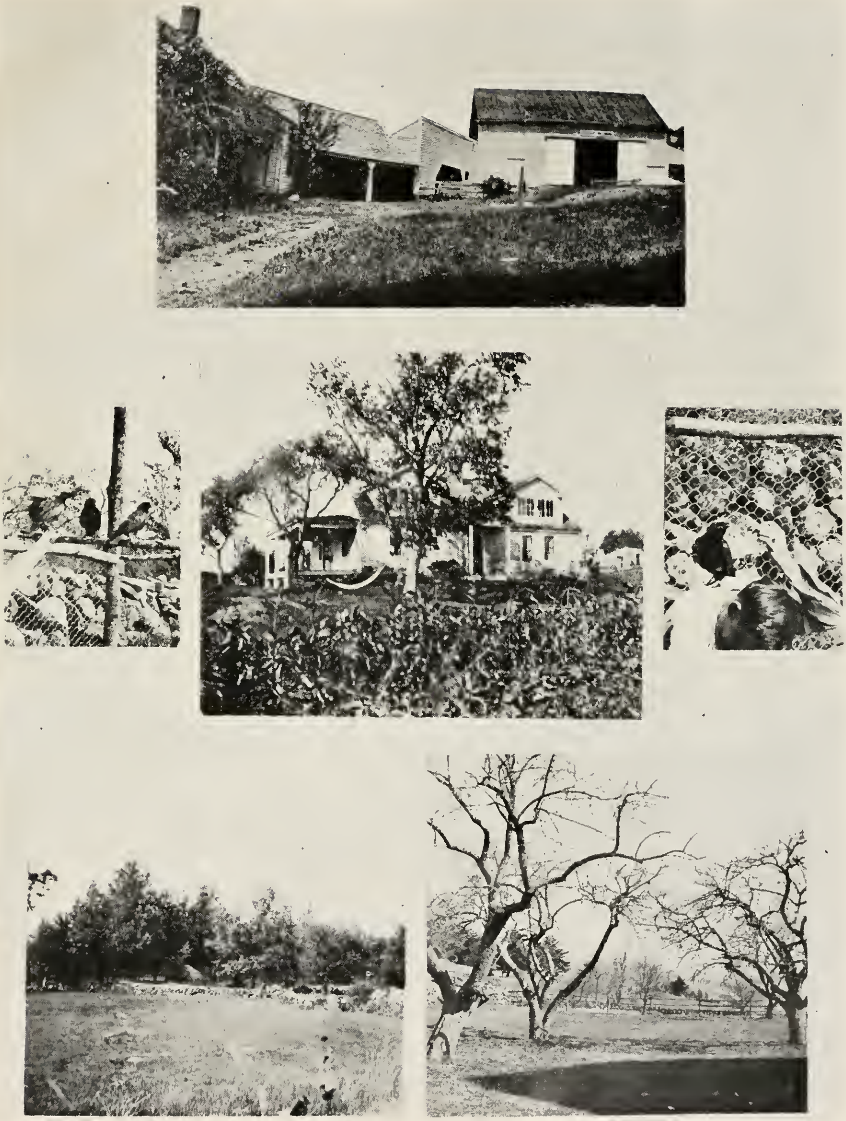


FIGURE 2. Views of the Franklin Field Station for the study of animal psychology.

of scores of invertebrates and vertebrates should not be observed under conditions of varying degrees of freedom. The country is already rich in animal life. Indeed, the Pemigewassett Valley, in which the station is located, is well-known to ornithologists because of the abundance of birds. It will undoubtedly prove feasible, as occasion arises, to import organisms for study.

The station is at present available during the months of June, July, August and September. It is at this time that work in Cambridge can least satisfactorily be conducted. The climate at Franklin is healthful and agreeable. For a few days in July the heat is at times oppressive, and before the end of September, frosts are likely to chill the enthusiasm of the field worker and to encourage his return to the city laboratory.

Only a small group of observers can be received at the Field Station during the summer. Each individual is responsible for his living expenses, and for the present at least, he must be responsible, also, for such expenditures as the conduct of his work demands. The station, as stated above, is the property of the writer, and is by him, in his capacity as director of studies in animal behavior at Harvard, placed at the service of a selected group of investigators during the summer.

Behavioristic work was initiated at the Franklin Field Station in the summer of 1912, by a study of habit-formation in earthworms, conducted by Ada W. Yerkes and the writer. This was a continuation of work begun previously in the Harvard Laboratory.

Two investigations were pursued during the second season (June to October, 1913) by Mr. C. A. Coburn and the writer. Of these, the one was a study of the transmission of savageness and wildness in mice, and the other, a naturalistic and experimental investigation of the behavior of the crow. The first of these was transferred for the season from the Harvard Laboratory. The second was a new inquiry which indeed could be conducted to advantage only at the Field Station. Both of these investigations prospered most encouragingly during the season, and we confidently expect and hope that they may be continued during the coming summer. Mr. Coburn, in a paper which appears in this number of the Journal (p. 185), has given a preliminary account of the results of certain of his experiments with crows. The naturalistic data which we obtained are reserved for later presentation in connection with observations which we hope to make next summer. This paper on the crow initiates a series of contributions from the Franklin Field Station which should, in invaluable ways, supplement our studies from the Harvard Laboratory.

THE BEHAVIOR OF THE CROW, *CORVUS AMERICANUS, AUD.*

CHARLES A. COBURN

From the Harvard Psychological Laboratory and the Franklin Field Station, Franklin, New Hampshire

Many years ago, Henry Ward Beecher remarked that if men were feathered out and given a pair of wings, a very few of them would be clever enough to be crows. This statement represents in a general way the opinion of the mental ability of the crow held by many students of bird life. The literature, both early and late, abounds with anecdotes depicting the intellectual superiority of the crow over other birds.

During the last two decades investigations have been made, by the United States Department of Agriculture and several state boards of agriculture, to determine whether the battle waged by the farmer against the crow is justified. The results of these studies tend to show that the value of the crow to the farmer by its destruction of injurious insects, mice and other rodents, more than compensates for the injury it does to the growing crops. These studies have also provided interesting data on the habits and mental characteristics of the crow. The data, derived in this manner, in no way contradict the general impression. It is, in general, indicated that the crow is very intelligent, supremely cautious and suspicious. Forbush[1] states that, in his opinion, it naturally is neither very cautious nor suspicious, but bold and fearless. Its apparent traits have been acquired by force of necessity. The reason for his statement is that on the Pacific Coast, especially during the early period of settlement, the crows were extremely bold and unsuspicious.

No definite study of the mental ability of the crow was made until 1910, when James P. Porter[2] used three crows in his investigation of intelligence and imitation in birds. His results did not put the crow on a higher plane of intelligence than several other birds, especially the English sparrow.

---

[1] Forbush, E. H. Useful Birds and their Protection. Published under the direction of the Massachusetts State Board of Agriculture. 1907.

[2] Porter, James P. Intelligence and Imitation in Birds: A Criterion of Imitation. *Amer. Jour. of Psychology,* 1910, vol. 21, pp. 1-71.

In co-operation with Professor Robert M. Yerkes, an investigation of the intelligence of the crow was begun in June, 1913, at the Franklin Field Station. Work was continued until late September. It is planned to continue the investigation in succeeding summers under the favorable conditions of the station.

The first summer's work included a general study of the habits and development of the bird (to be reported after additional data have been obtained) and a preliminary examination of its ability to discriminate brightnesses, sizes and forms.

It soon became apparent that the adaptation of an apparatus and method to the extremely wary and suspicious nature of the crow was a more difficult task than had been anticipated. This was accomplished after much experimenting with different methods of procedure and many changes in the apparatus. By the time both method and apparatus were fairly well adapted to the characteristics of the crow, the summer was well gone.

Our results are only approximations to the crow's discriminating ability. They are of value, however, in that they indicate certain important tendencies. A comparison of the results obtained during the first weeks with those obtained the last few days clearly shows the effect of improvement in method.

Two crows were used in these experiments. They were taken from a nest near the Field Station on the 6th of June. They were then, probably, about two weeks old. Number 1, a male, was larger and better developed when caught. When full-grown it was larger and bolder and less easily frightened than the female, Number 2.

For two or three weeks after they were caught, the young birds were fed earthworms, with an occasional bit of cooked cereal. Gradually this diet gave way to various kinds of meat, bread soaked in milk, cracked corn soaked in water, and table scraps.

The development, care, and feeding of young crows, will be discussed in a later paper.

When the two crows were about nine weeks old, they were able to fly a short distance and to eat alone. They were so tame that they recognized the voice of the experimenter and would come when called, perch on his arm or shoulder, and eat from his hand. This friendliness was shown to no other person, and an entire stranger would frighten them very much.

Four other crows were obtained from Pennsylvania, but they were too wild for use in the investigation.

The building, in which the experimenting was done, was divided into two compartments, each 10 feet by 12 feet. One of these served as a roost and feed-room. Adjoining this room was a fly, 24 by 10 by 8 feet high, made of chicken wire. The crows could fly direct from the roost to a perch in the far end of the fly.

The other compartment, which served as an experiment-room, was set off from the feed-room by a partition of chicken wire and a burlap curtain. The curtain could be pulled aside when experiments were not in progress, thus allowing a free circulation of air.

The apparatus used was a modified form of the discrimination-box used by F. S. Breed [3] and later by L. W. Cole [4] in their studies of the reactions of chicks to visual stimuli. The following description is intended to give only the essential points of the apparatus. For a more detailed account, reference may be made to the reports of Breed and Cole.

The entrance-chamber was a movable box 18 by 16 by 14 inches deep. The top, bottom, and three sides were of one-half inch boards. The fourth side was covered with wire netting, one-fourth inch mesh. In each end were openings, 7 inches by 9 inches, with horizontal slide doors.

Leaving the entrance-box, the crow entered the discrimination-chamber. This was 16 by 19 by 13 inches deep. The top was of wire, one-fourth inch mesh. Opening directly into this chamber were two chambers, 18 by 19 by 13 inches deep. The tops of these chambers were of wood as were also the sides and floors. The exit from each of these chambers was 7 inches by 9 inches, with horizontal slide doors. They opened directly into two exit-boxes similar to the entrance-box. The front ends of the stimulus-chambers were formed by a three-stimulus plate-shifter sliding in wooden tracks. For a minute description of this shifter, the reader is referred to the papers of Breed and Cole. The stimulus plates used in the experiments on size and form, were the standard plates devised by Yerkes and Watson[5] for their brightness vision apparatus and are described in detail in their paper.

---

[3] Breed, F. S. Reactions of Chicks to Optical Stimuli. *Jour. of Animal Behavior*, 1912, vol. 2, pp. 280-295

[4] Cole, L. W. The Relation of Strength of Stimulus to Rate of Learning in the Chick. *Jour. of Animal Behavior*, 1911, vol. 1, pp. 111-124.

The floor, walls, and top of the discrimination-chamber and the two stimulus-chambers were painted a dark gray. This rendered the two stimulus-chambers alike in every way except with respect to the desired difference in optical stimuli, namely, that of brightness, size, or form. Care was taken throughout the work to see that this was the only means by which the crow could choose the correct path.

The exit doors were operated by a system of cords. A curtain was suspended from the ceiling at the rear of the apparatus. The experimenter, standing behind the curtain and looking through a small peep-hole, could observe the behavior of the crow while in the apparatus and open and close the exit-doors without being seen by the crow.

Late in the summer, two swinging gates of wire were suspended between the discrimination-chamber and the two stimulus-chambers. These gates also were operated by cords. At the beginning of a test they were drawn up to the ceiling of the discrimination-chamber. The purpose of these gates was to prevent the crow from returning into the discrimination-chamber after it had made a wrong choice.

During the experiments on brightness discrimination, the apparatus faced a north window. With the beginning of the tests of size discrimination, it was shifted to face a larger south window. In this position, it remained during the rest of the season.

The ability of the crow to detect a slight change in the situation, together with its wary and suspicious nature, made it impossible to choose a method of procedure at the beginning and to adhere to it rigidly throughout the period of work. The method used at the beginning was evolved during the preliminary trials, when the first indications were received of what the crow might reasonably be expected to do. Various changes were made in this initial method until a reasonably satisfactory one had been developed.

---

[5] Yerkes, R. M., and Watson, J. B. Methods of Studying Vision in Animals. *Behavior Monographs*, 1911, vol. 1, no. 2, p. 23.

For several days previous to the first preliminary series, the crows were compelled to enter the discrimination-chamber in order to get their food. For this purpose the apparatus was placed before a small door in the partition separating the feed-room from the experiment-room. At first, the pan containing the food, was placed just inside the entrance door. Then, gradually, it was placed farther back until the crows were required to go through the discrimination-chamber, and the one or the other of the stimulus-chambers, into the exit-boxes. After a few days, they did this with no apparent fear.

The first preliminary tests were given on July 16th. The crows were then about nine weeks old. The standard stimulus plates had been removed from the stimulus shifter, leaving square openings, 12 cm. by 12 cm. Opal flashed glasses were placed in the slides immediately before these openings, so the illumination of the two chambers was the same.

The apparatus was adjusted with the entrance-box before the small door in the partition between the feed-room and the experiment-room. When one of the crows had entered this box to get the bit of food placed therein, both doors were closed and the entrance-box was then placed before the entrance to the discrimination-chamber. The door leading to the discrimination-chamber next was opened and the crow allowed to enter. The exit doors being open the crow could proceed to one of the exit-boxes and obtain food. The exit and entrance-boxes were now exchanged and the crow given another trial.

Both crows were much frightened by being confined in the entrance and exit-boxes. After two days, with nine such trials, they became somewhat calmer during the experiments. The exit doors were now closed and the crows allowed to enter the discrimination-chamber, go to one of the stimulus-chambers and there wait until the exit door was opened. This new situation, especially the opening of the exit door, frightened them as much as being shut in the entrance or exit-boxes had at the beginning. In the first trial they could not be induced to enter the discrimination-chamber until the exit doors were opened as before. However, after eight trials with the doors closed, they had lost much of their fear. In these seventeen trials, Number 1 went eleven times to the right and six times to the left. Number 2 went every time to the right.

When the crow chose the correct path, it was always rewarded with a bit of food,—a small piece of mouse, frog, or other meat. If it chose incorrectly, it received no food and was required to remain three or four minutes in the exit-box, which had been previously darkened by a cloth thrown over the wire side. The dislike of crows to remain in a darkened chamber was utilized also by the gradual darkening of the entrance-box when the crows hesitated too long before entering the discrimination-chamber at the beginning of a test. This never failed to cause them to leave immediately. There were, therefore, at least two motives for correct choice, namely, the desire for food and the dislike of the darkened box. The latter can be considered a constant factor, for they reacted to the darkened box as strongly at the end of the summer as they did at the beginning.

Care was taken throughout the experiments to keep the factor of hunger constant. It was impossible to do this at all times, and it is highly probable that the results in many cases were materially affected by the change in this factor.

In the beginning, two series of five tests each were given per day. The times for the beginning of these series varied slightly, but as a rule they were 7:30 A. M. and 1:00 P. M. The crows, with this number of tests, would still be hungry at the end of the series, so the number of tests per series was raised to ten and the amount of food given at the end of each correct choice was lessened. It soon became apparent that the crow, in this case, was confined too long. After the seventh or eighth test, it usually busied itself more with getting out of the apparatus than with choosing the correct path in order to get food. On this account, three series, (7:30 A. M., 12:00 M. and 4:00 P. M.), of eight tests each were given per day. Finally the number of trials in each series was changed to five, and this seemed to be the best solution of the problem, as the crows were sufficiently hungry three times a day to be eager to get food. In the majority of cases, they were still hungry at the end of a series. The time required for the five tests was rarely over ten minutes, and the crows, as a rule, did not become restless in this time.

As a rule, one crow was given all the trials of a series before the other was caught. In a few series, the crows were given alternate tests. This was not conducive to the best results, for the crow, waiting in the entrance-box until the other completed the test, would become so restless that in many cases it would begin to throw itself against the woven wire side of the box. By the time its turn came, the desire to escape from the box had entirely overcome the desire for food, and, as a result, it would rush through the test and recommence its struggle to free itself. If, by chance, it made a correct choice, the food would not be noticed.

The results of each series of tests were kept on record sheets similar to those used by H. C. Bingham [6] in his study of the perception of size and form in the chick. In addition to a record of the correct and incorrect choices, the time required for the choice and a sketch of the path of the crow were also recorded.

In the study of brightness perception, the apparatus remained as in the preliminary series except that the stimulus areas of the stimulus-chambers differed in intensity. This difference was obtained by the use of more or less opaque substances, namely, black cardboard, milk glasses, and paper. These were placed over the opal flashed glass of one of the stimulus areas. The slides, which held the plates of opal flashed glass before the stimulus areas, were large enough to admit also the cardboard, milk glasses, or sheets of paper.

Black cardboard was first used. Since it allowed no light to pass, the illumination of the stimulus area before which it was placed was practically zero. The crows, in the trial series, had become partially accustomed to stimulus areas of an intensity produced by light passing through but one thickness of opal flashed glass. Consequently in the brightness experiments, they avoided the darkened chamber. The chambers were darkened in no regular order, but in ten or twenty tests, one chamber would be darkened as many times as the other.

After fifteen tests with each crow, the cardboard was exchanged for two milk glasses, then later for one milk glass and finally for one sheet of paper. The difference in the intensity of the two areas in this last case was comparatively slight. With care it could be distinguished by the human eye.

Table 1 shows the results of these tests.

---

[6] Bingham, H. C. Size and Form Perception in *Gallus domesticus*. *Jour. of Animal Behavior*, 1913, vol. 3, no. 2, pp. 65-113.

TABLE 1

INTENSITY DISCRIMINATION

Date	No. of tests	Correct choices	
		Crow No. 1	Crow No. 2
Conditions of Discrimination			
Cardboard and opal flashed glass—Opal flashed glass			
July 19	5	5	5
“ 19	5	4	5
“ 20	5	5	5
Two milk glasses and opal flashed glass—Opal flashed glass			
July 21	5	5	5
“ 21	5	5	5
“ 22	5	4	5
One milk glass and opal flashed glass—Opal flashed glass			
July 22	5	5	2
“ 23	5	3	3
“ 23	5	4	4
“ 24	5	4	4
“ 24	5	5	4
“ 25	5	3	4
“ 25	5	4	5
“ 26	5	5	5
“ 27	5	4	5
“ 28	5	5	5
“ 28	5	5	4
One sheet of paper and opal flashed glass—Opal flashed glass			
July 29	5	4	3
“ 30	5	5	3
“ 30	5	5	3
“ 31	5	5	3
“ 31	5	5	4
Aug. 1	5	5	4
“ 1	5	5	5

These results are but roughly indicative of the crows' ability to distinguish differences in illumination. Accurate measurements of the birds' visual acuity was not the aim of our experiments.

The chief value of these experiments on the discrimination of intensity is the demonstration of the ease with which the crow is able to adapt itself to experimental conditions and to solve accurately one variety of problem.

With the beginning of the experiments on size discrimination, the apparatus was so shifted that the front end was immediately before a large south window. In this position it remained during the season. The only other change was the insertion of the standard stimulus plates in the stimulus shifter. Difference in the illumination of the stimulus areas was eliminated.

A 5 centimeter[7] circle versus a 2 centimeter[7] circle was chosen for the beginning of this study. The correct exit was indicated by the larger circle.

This change in the conditions of discrimination naturally threw the crows into confusion. They refused to enter the discrimination-chamber unless forced to do so by the darkening of the entrance-box. If this were done, they would pass to and fro before the two stimulus-chambers, but they would not enter far enough into either of them for the exit doors to be opened. The series of the first two days had to be interrupted on account of the crows' fright. On the third day no attempt was made to work. During the day the crows were fed somewhat less than the usual amount of food. The next morning (August 5th), they were tried with a 9 centimeter circle versus a 5 centimeter circle. By this change the illumination of the stimulus-chambers was made to approximate that to which the crows had become accustomed in the experiments on the discrimination of intensity. Their hunger, on this day, was great enough to overcome in large measure their fright. The results of this, and the remaining series on size discrimination are given in Table 2.

After one series with the 9 centimeter versus the 5 centimeter circle, a 2 centimeter circle was substituted for the 5 centimeter circle. The crows' behavior now became practically normal. The only significant difference from previous reactions was a greater hesitation in choosing. Before finally entering a chamber, they would often pass to and fro several times before the two stimulus-chambers, again and again starting to enter one chamber only to back out and go to the other. As appears in the table, crow no. 1 made twenty correct choices in succession, while crow no.. 2 succeeded in choosing correctly eighteen times in twenty. This sudden return of calm and controlled reaction and the high percentage of correct choices, were due probably to the fact that the illumination of the stimulus-chambers through the 9 centimeter and the 2 centimeter circles was closely similar to that in the experiments on intensity discrimination.

---

[7] Stimulus plates will be designated by the diameter or the side.

It seems probable that the birds were simply choosing the more highly illuminated stimulus-chamber, which, in every case, was also the one presenting the larger stimulus area. That they did not continue to use this cue is proved by experiments in which the large stimulus area, and irregularly the small one also, were darkened by placing one thickness of milk glass over the opal flashed glass. This enabled the experimenter in some tests to present two stimulus areas differing in size and intensity of illumination. Now the chamber illuminated by the larger circular area was the more intense, and now the one illuminated by the smaller area. Had the crows attempted to depend upon the illumination of the chambers, or on the relative intensities of the stimulus areas, instead of on their size, they certainly would have been confused. As a matter of fact, the change influenced markedly neither their behavior nor their percentage of correct choices.

The experiments on the perception of size were continued for twenty-five days. The results (Table 2) show that the crows

TABLE 2

PERCEPTION OF SIZE

Date	No. of tests	Correct choices Crow No. 1	 Crow No. 2
	Conditions of Discrimination		
	5 centimeter—2 centimeter circle		
Aug. 2	Crows frightened. Abandoned series.		
" 3	Crows frightened. Abandoned series.		
	9 centimeter—5 centimeter circle		
Aug. 5	5	3	4
	9 centimeter—2 centimeter circle		
Aug. 6	10	10	8
" 6	10	10	10
	5 centimeter—2 centimeter circle		
Aug. 7	10	10	10
" 7	10	9	10
" 8	10	9	9
" 8	10	7	10
" 9	10	5	9
" 9	10	10	9
	5 centimeter—3 centimeter circle		
Aug. 10	10	8	9
" 11	10	8	7
" 11	10	9	10

TABLE 2—*Continued*

		Correct choices	
Date	No. of tests	Crow No. 1	Crow No. 2
	Conditions of Discrimination		
	3 centimeter—2 centimeter circle		
Aug. 12	10	9	7
“ 13	8	4	4
“ 13	10	6	7
“ 13	8	8	5
“ 14	8	6	6
“ 15	7	6	6
“ 15	9	7	8
“ 15	8	5	5
“ 16	8	7	5
“ 16	8	8	8
“ 16	8	6	5
“ 17	8	6	4
	5 centimeter—3 centimeter circle		
Aug. 17	8	8	6
“ 18	8	8	8
“ 19	5	3	3 (Left habit)
“ 19	6	4	6
“ 20	10	4 (Left habit)	8
“ 20	10	8	9
“ 20	10	7	10
“ 21	10	9	10
“ 21	10	5 (Left habit)	9
“ 21	5	3	5
“ 22	8	7	7
	6 centimeter—3 centimeter circle		
Aug. 22	8	8	7
	5 centimeter—3 centimeter circle		
Aug. 22	8	6	8
“ 23	8	3 (Left habit)	8
“ 23	8	6	7
“ 24	10	9	6
“ 24	10	10	9
“ 25	10	9	9
“ 25	10	9	9

improved surprisingly little with practice. The percentage of correct choices with the 5 centimeter versus the 3 centimeter circle was as low during the last few days of the training as it was on August 10th and 11th when they were first required to distinguish between these circles.

Throughout these experiments, the behavior of the crows while working was very erratic. Some days they worked slowly and carefully. Sudden noises, such as those caused by the opening or closing of an entrance or exit door, did not greatly disturb them. The results on these days of calm steadiness, as a rule, showed an increase in the number of correct choices. On other days, their behavior would be practically the opposite. While still in the entrance-box they would walk impatiently to and fro before the woven wire side of the box. When the entrance door was opened, they would often start several times to enter only to turn back into the entrance-box. When they finally did enter, they would rush to one of the exit doors, and, in a crouching attitude, wait until it was opened. On these days, great care had to be taken in opening and closing the doors for an unusual noise or sudden movement would greatly increase their excitement. During this behavior they were very likely to develop a position habit. Series, in which this excited behavior resulted in a considerable number of incorrect choices, have been noted in the tables.

The ability of the crow to pass directly from one set of circles to another with no great difference in the number of correct choices (see Table 2), was further tested by a series of experiments, the results of which appear in Table 3.

In these experiments, the attempt was made to determine whether the crows were reacting to a certain specific stimulus, or whether they were reacting to it because of its relation to another stimulus. For instance, if the 6 centimeter and the 4 centimeter circles were presented, and the crow trained to react positively to the 6 centimeter circle, would it continue to do so when the 6 centimeter circle was presented with a 9 centimeter circle, or would it, instead, choose the larger area in each instance?

As in the preceding series the crows were trained to choose the larger of two circles. When they had gained the ability to choose correctly, they were given ten trials with a different pair of circles. During these ten trials, they were rewarded after each test, regardless of the correctness or incorrectness of the reaction. A reaction was considered correct if the crow chose the larger circle. These series are designated, in Table 3, " relative reactions." The training series which preceded the relative series of August 26th are given in Table 2.

The results of these experiments indicate fairly clearly the relativity of the crows' reactions. Especially is this true of crow no. 1. For example, on August 24th and 25th, when the

3 centimeter circle was presented with the 5 centimeter circle, the crow reacted to the 3 centimeter circle thirty-seven times negatively and three times positively. On August 26th, the 3 centimeter circle, displayed with the 2 centimeter circle, was reacted to positively in every case. The results for crow no. 1 with the 6 centimeter circle when displayed with the 4 centimeter and the 9 centimeter circles, on August 26th and 27th, were almost as decisive.

TABLE 3

REACTIONS TO RELATIVE SIZES OF CIRCLES

		Correct choices	
Date	No. of tests	Crow No. 1	Crow No. 2
Relative reactions, 3 centimeter—2 centimeter circle			
Aug. 26	5	5	5
" 26	5	5	3
Training series, 6 centimeter—4 centimeter circle			
Aug. 26	10	7	9
Relative reactions, 9 centimeter—6 centimeter circle			
Aug. 27	5	4	2
" 27	5	5	3
Training series, 6 centimeter—4 centimeter circle			
Aug. 27	8	2	5
" 28	10	6	8
" 28	8	5	3 (Right habit)
" 29	5	4	4
" 29	5	4	3
" 29	6	5	5
Relative reactions, 3 centimeter—2 centimeter circle			
Aug. 30	5	5	2
" 30	5	5	4
Training series, 6 centimeter—4 centimeter circle			
Aug. 30	5	5	2
Relative reactions, 9 centimeter—6 centimeter circle			
Aug. 31	5	2	4
" 31	5	4	3

Only one day intervened between the conclusion of the tests of the relativity of the reactions and the beginning of experiments to determine the ability of the crow to distinguish circles from triangles, squares and hexagons.

With the beginning of this study of form perception the experimenter became more convinced than ever that the results, obtained in the previous experiments, did not truly indicate the crows' intelligence. A new form of reaction now developed. When either of the crows had made an incorrect choice and the exit door was opened, showing a dark exit-box, instead of entering as they hitherto had done, they would whirl about and quickly go to the other exit and there wait, even for five or ten minutes, until the door was opened. This behavior naturally tended to lower the percentage of correct choices.

The experimenter first tried to overcome this difficulty by having the exit-box illuminated until they had entered it. Crow no. 2 would always enter the box under these conditions, but crow no. 1, after a few trials, refused to enter either box unless there was a bit of food in view.

To meet this difficulty, the gates, described on page 188, were constructed. When the crow entered the wrong stimulus-chamber, the exit door was opened and at the same moment the gate between that chamber and the discrimination-chamber was dropped, thus preventing the crow from escaping to the other exit. The dropping of the gate tended to frighten them somewhat, so they always quickly entered the exit-box, which was again darkened as in the early experiments. The effect of this improvement in the apparatus on the behavior of the crows appears in the results of Table 4.

The crows had been given one hundred and six tests for their ability to distinguish a 6 centimeter circle from an 8.081 centimeter triangle. During these trials no appreciable increase in the percentage of correct choices had been made. Immediately after the gates were brought into use, improvement commenced and thereafter the majority of the choices were correct. Crow no. 2 did not make quite as high a percentage of correct reactions as did crow no. 1. This was probably because no. 2 seemed to be more frightened by the dropping of the gate. If an incorrect choice was made early in a series, there was a tendency, on the part of no. 2, to avoid that stimulus-chamber during the remainder of that series.

The 6 centimeter circle, the 8.081 centimeter triangle, the 5.317 centimeter square, and the 3.29 centimeter hexagon are of equal area. The last thirty tests were with figures unequal in size. The 6 centimeter and the 9 centimeter circles each possess a greater area than the 3 centimeter hexagon, whose area, in turn, is almost twice as great as that of the 3 centimeter circle.

TABLE 4

Discrimination of Form

Date	No. of tests	Correct choices Crow No. 1	Correct choices Crow No. 2
Conditions of Discrimination			
6 centimeter circle—8.081 centimeter triangle			
Sept. 2	6	5	3
" 2	5	4	3
" 3	5	3	4
" 3	5	4	3
" 3	5	4	3
" 4	5	4	2
" 4	5	5	2
" 4–8	45	39	32
" 8	5	5	2 (Right habit)
" 8	5	3	4
" 9	5	3	4
" 9	5	3	5
" 10	5	3	1 (Left habit)
" 10	5 (Began using gates)	3	5
" 11	5	5	4
" 11	5	5	5
" 11	5	3	5
" 12	5	5	4
" 12	5	5	5
" 12	5	5	5
6 centimeter circle—8.081 centimeter triangle (Inverted)			
Sept. 13	5	5	5
6 centimeter circle—5.317 centimeter square			
Sept. 13	5	5	5
" 13	5	5	5
" 14	5	5	3 (Left habit)
" 15	5	5	5
6 centimeter circle—4.243 centimeter square			
Sept. 15	5	5	5
" 15	5	4	5
" 16	5	5	5
6 centimeter circle—3.29 centimeter hexagon			
Sept. 16	5	4	4
6 centimeter circle—3.00 centimeter hexagon			
Sept. 16	5	5	5
" 17	5	5	4
3 centimeter circle—3.00 centimeter hexagon			
Sept. 17	5	5	3
" 18	5	5	2 (Left habit)
9 centimeter circle—3.00 centimeter hexagon			
Sept. 18	5	5	4
" 18	5	5	5

The intensities of the stimulus areas and the general illumination of the chambers were varied in these tests by the use of milk glasses as described on page 194. The only visual factor which was constant during the thirty trials, was that of form. It is evident, therefore, that this was the cue which enabled crow no. 1 to make a perfect record in these series.

Lack of time prevented further work on the perception of form. The last two days of work were devoted to a further study of size discrimination. The purpose was to obtain, if possible, more conclusive evidence of the crows' ability to distinguish sizes, and, incidentally, to learn if the improvement in the method (introduction of gates) would increase the percentage of correct reactions to differences in size.

Thirty tests were given, the results of which appear in Table 5. During the first series, the crows appeared to be confused by the sudden change in the problem presented to them. They worked rather slowly and quietly, but their choices were not made with the usual definiteness. It was evident that they (especially crow no. 1), did not clearly appreciate what was required of them.

TABLE 5

DISCRIMINATION OF SIZE

Date	No. of tests	Correct choices Crow No. 1	 CROW No. 2
	Conditions of Discrimination		
	5 centimeter—3 centimeter circle		
Sept. 19	10	4	7
" 19	5	5	4
	5 centimeter—4 centimeter circle		
Sept. 19	5	5	5
	5 centimeter—4.5 centimeter circle		
Sept. 20	5	4	4
" 20	5	5	5

In the second series, the indefiniteness and hesitation in their behavior were lacking. In every case no. 1 went quickly and directly to the correct exit. Crow no. 2 made a mistake in the first test. Its decisions, however, were made clearly and definitely thereafter. This clear-cut, decisive type of reaction continued, with both crows, during the remaining tests, even when the discrimination was between the 5 centimeter and the

4.5 centimeter circles. If quickness of choice can be taken as a measure of the ease of discrimination, it is probable that the crows are capable of distinguishing much smaller differences.

The crow deserves its reputation. It is an exceptionally interesting subject for the behaviorist and worthy of his greatest skill. As has been indicated earlier in this report, it is planned to observe systematically crows at the Franklin Field Station, both in the field and in the laboratory, in order that a reasonably complete and reliable description of their behavior may be given. Because of the division of labor among a number of observers, it will be necessary to publish reports from season to season instead of reserving all materials for a monograph. The present paper is indicative of some of the chief characteristics of the bird, and suggestive of experimental difficulties. Another season should prepare us to report on the habits, instincts, and development.

SOME RELATIONS BETWEEN RHEOTAXIS AND THE RATE OF CARBON DIOXIDE PRODUCTION OF ISOPODS

W. C. ALLEE
Thompson Biological Laboratory, Williams College
AND
SHIRO TASHIRO
Laboratory of Biochemistry and Pharmacology, the University of Chicago

For several years one of us has been working upon an analysis of the rheotactic reaction of the isopod, *Asellus communis*, Say. In the course of this work it became evident that certain conditions known to affect animal metabolism likewise regularly affected the rheotactic reaction of isopods. Thus it was found that low oxygen tension, high carbon dioxide tension, chloretone, potassium cyanide, lowered temperature, sudden extreme increase of temperature, starvation, and fatigue decreased the percentage of positive rheotactic responses given. On the other hand caffein, increased oyxgen tension, and a gradual increase of temperature had the opposite effect. (Allee, '12, '13.)

When the rate of metabolism of isopods was determined by their resistance to potassium cyanide (Child, '13, '13a; Allee, '14; also page 206.) isopods giving a high percentage of positive rheotactic responses in a circular current had the highest rate of metabolism. Those with a high per cent. of negative responses were second, while those with a low positive response and with either the negative or indefinite reaction dominating had the lowest rate of metabolism.

For a number of years the other of us has been working upon a method for determining with analytical accuracy the minute amounts of carbon dioxide given off in the metabolism of nerve fibers. (Tashiro, '13, '13a, '14.) The apparatus devised will detect and measure with accuracy 0.000,000,1 gram of carbon dioxide.

For those who are not familiar with the new method for determining carbon dioxide we may say that the quantitative method depends upon determining the minimum amount of gas which will give the first precipitate of barium carbonate when introduced into a chamber in which a perfectly clear drop of barium hydroxide is exposed. It was previously found by work with known amounts of very dilute carbon dioxide that the minimum amount of carbon dioxide which gives the first precipitate is 0.000,000,1 gram. Thus, by determining the minimum number of cubic centimeters of a gas from a respiratory chamber of known volume, we can calculate very accurately the amount of carbon dioxide given off by the tissue or animal under observation.

The details of the method are as follows: An animal is left in the respiratory chamber (15 cc. capacity) for a respiration period of ten minutes. Then this air is driven into a gas pipette. After cleaning and washing the apparatus one cubic centimeter of this gas is introduced into the barium hydroxide chamber but gives no precipitate; .25 cc. more is introduced with no result; .25 cc. more gives a precipitate. The total volume introduced, 1.5 cc. is the minimum volume that will give the first precipitate. Since 0.000,000,1 gm. of carbon dioxide is the minimum amount which gives the first precipitate, it is certain that 1.5 cc. of respired air must contain 0.000,000,1 gm. of carbon dioxide. The total respiratory chamber must have contained $\frac{15}{1.5}$ x 0.000,000,1 or 10 x 10^{-7} grams carbon dioxide.

Not all of the work to be reported in this paper was done in this detailed quantitative manner since in some cases only comparative results were needed. For the comparative work a piece of apparatus called a Biometer[1] (Tashiro, '13.) was used. This consists essentially of two chambers of equal size which are prepared for a determination in exactly the same manner and the animals to be tested for relative carbon dioxide production are inserted. At the start each chamber contains a perfectly clear drop of barium hydroxide. The chamber which first shows a precipitate of barium carbonate and which later shows more precipitate evidently has had carbon dioxide produced at a higher rate than the other chamber. Hence it is easy to find which of two isopods is producing the greater amount of carbon dioxide.

---

[1] Quantitative determinations can also be made with the Biometer by using one chamber as a respiration chamber and the other for the determination.

THE PROBLEM

With this more refined method of obtaining an insight into the relation between physiological states and animal behavior the following three lines of inquiry were prosecuted during the time at our disposal at Woods Hole during the summer of 1913:

1. What is the relation between the rate of carbon dioxide production of isopods and their resistance to relatively strong solutions of potassium cyanide?
2. What is the effect of the calcium ion upon carbon dioxide production and rheotaxis in isopods?
3. Is there a relationship between the variation in carbon dioxide production and the rheotactic reaction of isopods?

THE STOCK

Isopods from a series of collections from small fresh water ponds near Woods Hole, Massachusetts, were used in these experiments. They were all *Asellus communis*, Say, and were about half grown. The isopods came from silt and debris bottomed ponds and were kept under comparable conditions in the laboratory.

METHODS

The isopods were tested for their rheotactic reaction in a circular current the bottom of which was covered with wax. The responses of an individual isopod for ten successive minute reaction periods were taken as a fair indication of the rheotactic tendencies of the animal. The isopods were judged to give a positive reaction when they went against the current for over half of the minute's reaction period. They were considered to give a negative reaction when they moved with the current for over half of their minute's trial and indefinite when their movements gave no indication of being regulated by the direction of the current. The approximate distance covered by each reaction was recorded and will be found in a standardized form in the tables under the head of efficiency in the current. In general the movements of highly positive isopods are more vigorous than those of negative isopods, which in turn are more vigorous than those giving an indefinite reaction. (For further details see Allee, '13.)

When the carbon dioxide output was to be tested the isopod was dipped into water free from carbon dioxide, dried momentarily on filter paper and placed on a cover glass with no water added except that which clung to the animal. An amber ring about three millimeters high was placed around the isopod and this was covered with wire gauze to prevent extended movement of the animal while in the respiration chamber.[2] This precaution was the more effective since isopods are strongly positively thigmotactic and will rest quietly for extended periods when they are able to place their bodies in an angle of their container.

When comparisons were made in the Biometer, isopods of approximately the same size were selected in order to guard against a greater production of carbon dioxide due to greater mass. The isopods were left in the respiration chambers for only ten minutes during the quantitative work but in the qualitative results, tested in the Biometer, the isopods were left as long as thirty minutes. The fact that isopods survived nine daily tests and showed no ill effects of the handling demonstrates there is little danger to the animal in such treatment.

THE RELATION BETWEEN CARBON DIOXIDE PRODUCTION AND RESISTANCE TO POTASSIUM CYANIDE

The work upon the relation between carbon dioxide output and the resistance of isopods to potassium cyanide was qualitative only and was carried on to ascertain whether or not the resistance of isopods to the cyanide is a safe index of their metabolic activity. Child ('13, '13a) found that in Planaria the susceptibility of animals or pieces of animal to 0.001 mol. solution of potassium cyanide varied in general with the rate of metabolism. Estimation of carbon dioxide production on individuals and pieces (of the same species) made at Dr. Child's request by Tashiro with the aid of his Biometer showed that carbon dioxide production ran parallel with susceptibility to potassium cyanide, and so afforded a confirmation of Child's conclusion concerning the relation between susceptibility and the rate of metabolism.

---

[2] We appreciate the roughness of this method for checking spontaneous muscular movement, but it was out of consideration for us to devise an automatic recorder for bodily activity such as is necessary in order to make accurate metabolism experiments with mammals. The principal source of error in determining the amount of carbon dioxide given off by isopods lies in the fact the spontaneous muscular movements were not under complete control. With the device described above and by constant, careful observation with a hand lens of the animal during the experiment, we convinced ourselves that we had sufficient control of the movements of the animals to answer the needs of our experiments.

Allee has conducted a series of tests to find whether or not Child's cyanide resistance method would apply to isopods and has found decided evidence that the application is possible. (Allee, '14.) As a final check upon this work we repeated with isopods the tests of the relation between carbon dioxide production and cyanide resistance that had been made earlier for Planaria.

The detailed method of procedure was as follows: Two easily distinguished isopods of equal size, whose rheotactic reaction had been previously tested by Allee, were placed in the Biometer by Tashiro and the relative speed of carbon dioxide output was determined. Immediately upon the removal of the

TABLE 1

Showing the relation between the rheotactic reaction, carbon dioxide production and resistance to 0.001 mol. potassium cyanide. The carbon dioxide output was compared in the biometer and the total reactions of two animals thus compared are shown in each horizontal division of the table.

Isopod No.	Rheotactic reaction in percentage of total number of trials				Efficiency in the current	Carbon dioxide output compared	Survival time in .001 mol. KCN. in hours and minutes	Sex	Length in mm.
	+	—	∞	0					
92	60	20	20		2.1	more	2:10	♂	6.5
89	0	70	30		2.0	less	3:10	♂	6.0
86	100	0	0		2.1	more	2:00	♂	5.0
87	100	0	0		2.2	less	2:30	♀	7.0
90	80	10	10		2.1	more	2:00	♂	6.5
91	80	10	10		2.0	less	2:30	♀	5.5
95	100	0	0		2.6	more	5:30*	♂	7.0
94	20	80	0		2.2	less	4:45	♂	5.0
30	70	20	10			more	2:20	♂	4.5
169	40	20	40			less	3:10	♂	5.0
84	10	0	40	50		less	2:55	♂	6.0
171	60	40	0			more	1:35	♂	5.5

* See discussion, page 207.

isopods from the respiration chamber they were placed in an Erlenmeyer flask in 0.001 mol. solution of potassium cyanide and their survival time was ascertained by Allee. It should be noted that the experimenter on the determination of the carbon dioxide output was ignorant of the behavior of the animals, thus eliminating any prejudice for the determinations. The results of experiments of this character are shown in table 1.

The table shows that in ten of the twelve isopods tried the evidence from the survival time ran parallel with that of the carbon dioxide production, that is, the isopods giving the more carbon dioxide had the shorter survival time in the cyanide. The table also shows that where there was a difference in the rheotactic reaction of the animal tested, the more carbon dioxide was given by the isopod that gave the higher percentage of positive rheotactic reactions. (Cf. page 213; also Allee, '14.) In the case of isopods No. 94 and 95 where the isopod that gave off less carbon dioxide lived a shorter time in the cyanide the experimental records show that No. 95 moved more in the respiration chamber than did No. 94 and also that it was two millimeters longer. Either of these factors might account for the discrepancy. If the potassium cyanide resistance in this case is taken as the true index of the metabolism it will be noted that the animals living longer, i.e., having the lower rate of metabolism gave the highest percentage of positive rheotactic reactions. This apparent contradiction will be discussed later (page 211).

Since in 83% of the cases tried the carbon dioxide production tallied exactly with the resistance to potassium cyanide and in the other 17% of the cases the apparent exception is capable of reasonable explanation, it seems safe to conclude that so far as carbon dioxide production is concerned the resistance of isopods to potassium cyanide is a safe index of the metabolic activity of the animals.

THE EFFECT OF THE CALCIUM ION UPON RHEOTAXIS AND CARBON DIOXIDE PRODUCTION

In connection with experiments on irritability Tashiro has studied the effects of inorganic salts upon tissue metabolism. Whatever the mechanism of the effect of such salts on tissues

TABLE 2

Showing the effect of calcium chloride upon carbon dioxide production and rheotaxis in isopods. The survival time in potassium cyanide is added for comparative purposes. The isopods were first tested for rheotaxis, then two of approximately the same size were taken for determination of their carbon dioxide output in the biometer. The one of these that gave the least carbon dioxide was taken as a control, its rheotactic reaction was again tested and it was allowed to stand in water to which it was accustomed while the other was treated.

The second isopod, the one giving the most carbon dioxide, was placed in a 0.16 mol. solution of calcium chloride until the positive rheotactic tendency was markedly decreased. Immediately afterward the carbon dioxide production of the two was again compared in the biometer.

Isopod No. 30	Isopod No. 169
Rheotaxis test, 11:55 A. M. Temp. 20	Rheotaxis test, 12:25 P. M. Temp. 20
50%+, 50%—; Efficiency, 2.1	90%+, 10%—; Efficiency, 2.1
Tested in Biometer 1:47-2:00 P. M. Temp. 23.5	Tested in Biometer 1:47-2:00 P. M. Temp. 23.5
Less CO_2 than No. 169	More CO_2 than No. 30
Rheotaxis test 2:00 P. M.	Put in 0.16 Mol. $CaCl_2$ 2:05 P. M.
70%+, 20%—, 10%∞; Efficiency, 2.25	Rheotaxis test 2:07 P. M.
	80%+, 20%— Efficiency, 1.6
	Rheotaxis test 2:27 P. M.
	40%+, 20%∞, 40%o; Efficiency, .95
	Taken from $CaCl_2$ 3:43 P. M. In $CaCl_2$ 36 minutes
Tested in Biometer 3:44-3:57 P. M.	Tested in Biometer 3:44-3:57 P. M.
More CO_2 than No. 169	Less CO_2 than No. 30
Survival time in 0.001 Mol. KCN 2 hours, 20 minutes	Survival time in 0.001 Mol. KCN 3 hours, 10 minutes
♂, 4.5 mm. long	♂, 5.0 mm. long
Isopod No. 171	**Isopod No. 84**
Rheotaxis test 12:25 P. M. Temp. 20	Rheotaxis test 12:00 M. Temp. 20
10%+, 90%—; Efficiency, 2.4	30%+, 60%—, 10%∞; Efficiency, 2.6
Tested in Biometer 2:49-3:05 P. M.	Tested in Biometer 2:49-3:05 P. M.
Little CO_2 given off	Little CO_2 given off.
Less CO_2 than No. 84	More CO_2 than No. 171
Rheotaxis tested 3:50 P. M.	Put in 0.16 Mol. $CaCl_2$ 4:02 P. M.
60%+, 40%—; Efficiency, 2.0	Rheotaxis tested 4:07 P. M.
	10%+, 40%∞, 50%o; Efficiency, 0.9
	Taken from $CaCl_2$ 4:27 P. M. In $CaCl_2$ 25 minutes
Tested in Biometer 4:35-5:12 P. M.	Tested in Biometer 4:35-5:12 P. M.
More CO_2 than No. 84	Less CO_2 than No. 171
Survival time in 0.001 Mol. KCN 1 hour, 35 minutes	Survival time in 0.001 Mol. KCN 2 hours, 55 minutes
♂, 5.5 mm. long	♂, 6.0 mm. long

may be, it was clearly proven (Tashiro, '13), that inorganic salts which affect physiologic states of the nerve equally modify metabolism as measured by the carbon dioxide production. With Dr. Lingle[3] he has further extended the study of the effects of calcium and sodium ions upon tissue metabolism upon isolated pieces of heart tissue of turtles.

Allee[3] has spent considerable time upon the effects of certain inorganic salts upon the rheotactic reactions of isopods and found among other results that calcium chloride caused animals that were highly positive to a water current to become much less positive. That the calcium rather than the chlorine ion is responsible for these results is shown by tests with a number of other inorganic chlorides some of which increase while others decrease the positiveness of the rheotactic reaction of isopods.

From his work on tissue metabolism Tashiro suggested that the calcium chloride in some way caused a decrease in the metabolic activity of the isopods. In order to test this the crucial experiments were made the results of which are exhibited in table 2.

Although only two comparisons were made yet the results are so diagrammatic and are so fully in accord with the previous experience of both authors that they may fairly be taken as giving a truthful picture of the conditions under consideration.

In brief the experiments were as follows: Two isopods of approximately the same size were tested for their relative rate of carbon dioxide production in the Biometer. The isopod having the lower rate of carbon dioxide output was taken as a control and was again tested for the rheotactic reaction and then left in conditions to which it was acclimated while the other was treated. The second individual, which had the higher rate of carbon dioxide production was placed in a 0.16 mol. solution of calcium chloride until the tendency to give a positive rheotactic reaction was markedly reduced. Then the rate of carbon dioxide production of the two was again tested in the Biometer.

In both pairs tested the isopod with the higher rate of carbon dioxide production at the first test in the Biometer had also given the higher percentage of rheotactic responses, but after being treated with calcium chloride for 25-36 minutes it came to be less positive in its rheotactic reaction, and also gave less carbon dioxide and was less susceptible to potassium cyanide than the control individual. In other words the calcium chloride (0.16 mol.) decidedly decreased the rate of metabolism of the isopods and also reduced their tendency to give a positive rheotactic reaction.

---

[3] Unpublished results.

TABLE 3

Showing the quantitative daily determination of the carbon dioxide output of isopods Nos. 102 and 12. Isopod No. 12 was tested quantitatively for carbon dioxide production in the biometer; isopod No. 102, in a new apparatus especially devised for quantitative work. Column 3 gives the capacity of the respiratory chamber; column 4 shows the number of cc. of respired air which first gave the precipitate of BaCO$_3$; column 5, the amount of CO$_2$ given by the isopod in ten minutes, for method of calculation see page 203.

Date	Temperature in degrees C.		Volume of respiratory chamber		Minimum cc. giving Ppt. of BaCO$_3$		Amount of CO$_2$ given by isopods during 10 minutes in gms.	
1	2		3		4		5	
Iso-pod No.	12	102	12	102	12	102	12	102
Aug. 14	23	22.5	15	25	1.5	.75	10×10^{-7}	33×10^{-7}
15	23	23	15	25	1.6	.4	9.3×10^{-7}	62.5×10^{-7}
16	23.5	23.5	15	25	.55	.5	27.2×10^{-7}	50×10^{-7}
17	24.5	24	15	25	1.8	.4	12.2×10^{-7}	62.5×10^{-7}
18	24	24	15	25	1.4	2.0	10.7×10^{-7}*	12.5×10^{-7}*
19	No determination.†							
20	20.5	20	15	25	7.1	1.6	12.1×10^{-7}	15.6×10^{-7}
21	22.5	20.5	15	25	1.4	.7	10.7×10^{-7}	35.7×10^{-7}
22	22.5	22.5	15	25	.5	1.1	30×10^{-7}	22.7×10^{-7}

* Determination in some doubt due to lack of facilities for running a duplicate determination.

† No determination because of lack of carbon dioxide free air which is required n preparing the apparatus for a determination.

THE RELATION BETWEEN DAILY VARIATION IN CARBON DIOXIDE PRODUCTION AND THE RHEOTACTIC REACTION

It has been observed that the rheotactic reaction of isopods varied to a considerable degree even when the animals were kept under approximately identical external conditions. (Allee, '13.) In order to analyze this behavior it is necessary to follow the variations in the daily metabolism which obviously cannot be done by the cyanide method because that depends on the death point of the animals. Daily determination of the carbon dioxide output of the isopods in connection with a daily test of the rheotactic reaction proved feasible. The carbon dioxide determinations were made by Tashiro in the manner already given (page 203). The rheotactic reactions were tested by Allee and neither knew the results of the other until the end of the tests. The results obtained are listed in tables 3 and 4.

From the results exhibited in table 4 it is seen that with both isopods No. 102 and No. 12 six of the seven changes of carbon dioxide production and the rheotactic response run in a parallel direction. This means that with these two isopods 86% of the variations in carbon dioxide output and rheotactic reaction were similar. The amount of variation is not always proportionate but it should be remembered that the isopods were able to move to a limited degree in the respiration chamber and that this caused an increase in the carbon dioxide production that was not controlled. Also there is a possible error of about 5% in the method of ascertaining the sign of the rheotactic reaction. (Allee, '12.) In view of these considerations the experimental results are about all that could be expected and are certainly more exact than any previous observation on the correlation of the behavior of animals upon their metabolic rate or physiological state.

Incidentally the table shows an agreement in the direction of variation of carbon dioxide production and the oxygen tension in the water in which the isopods were kept in 66% of the cases. The variations in the rheotactic response and oxygen tension agree in 73% of the cases. This seems to be good evidence that all three of these factors are more or less closely related.

The evidence here presented also makes it apparent that each individual isopod has in all probability a different rate of metabolic activity from that of any other isopod, (cf. Allee, '14) and farther that it is not a fixed standard of metabolism that accompanies a high degree of positiveness in the rheotactic response but rather a relative rate. Thus on the average isopod No. 102 (length 8 mm.) gave off over twice the amount

TABLE 4

Showing the relation between daily variations in carbon dioxide production and rheotactic reactions of isopods Nos. 102 and 12. The amount of carbon dioxide given in ten minutes may be obtained in grams by multiplying the numbers given in the second column by 10^{-7}. In the third column + indicates the results are what would be expected from our present knowledge of the rheotactic reaction if there is a direct relation between the rate of positiveness in the water current and the rate of carbon dioxide production; — indicates the opposite state of affairs. Two oxygen tensions are given; the first being that from which the isopods were taken before their rheotactic test; the second represents that in which they were placed after the carbon dioxide determination. Between testings the isopods were kept in one liter Erlenmeyer flasks which were full of water and tightly corked.

ISOPOD NO. 102

Date	CO_2 produced in 10 min. See above	Expectation	Rheotactic reaction in per cent of total trials				Efficiency in current	O_2 tension before trial	O_2 tension at start of daily interval	Temperature in degrees C.
			+	—	∞	0				
Aug.										
14	33		30	40	30		2.4	1.2	2.5	19
15	62.5	+*	20	70	10		2.3	1.8	3.0	19
16	50	—‡	60	20	20		2.4	2.35	2.35	19.5
17	62.5	+	70	10	20		3.0	1.7	2.6	21.5
18	12.5	+	40	40	20		3.0	2.5	1.9	20.5
19	....†				10	90	0.1	0.0	1.0	21
20	15.6	+		10	60	30	0.8	0.0	5.+	20
21	35.7	+	60	40			2.5	5.4	5.4	20
22	22.7	+	50	40	10		2.1	4.4	4.4	22.5

ISOPOD NO. 12

Aug.										
14	10		100				2.4	0.6	2.5	20
15	9.3	+	50	30	20		2.2	2.23	3.0	20
16	27.2	+	60	10	30		2.6	2.79	2.79	21.5
17	12.3	—‡	90		10		2.5	2.0	2.6	21.5
18	10.7	+	60	10	30		2.4	1.9	1.9	20.5
19	....†				90	10	1.3	0.0	1.0	20
20	2.1	+				100	0.0	0.0	5.+	20
21	10.7	+	50	30	20		1.45	5.4	5.4	20
22	30.0	+	70	10	20		2.0	4.4	4.4	22.5

* The increase in negativeness and decrease in indefiniteness indicate an increased rate of metabolism. (Allee, '14);

† No determination due to technical difficulties with the apparatus; carbon dioxide production in all probability very low.

‡ More work is needed before an explanation of these results can be offered.

of carbon dioxide per ten minute respiration period than did No. 12 (length 7 mm.). After making all due allowance for the effect of the slight size difference No. 102 had the higher metabolic activity yet the average percentage of positive rheotactic reactions was lower than with No. 12. Also the pair of isopods Nos. 86 and 87 (table 1, page 206) gave identical rheotactic responses but the carbon dioxide production and resistance to potassium cyanide both indicate a difference in the metabolic activity of the two animals. The same is true of isopods 90 and 91.

So far as the facts at present are known it appears that the relation between metabolic activity and the rheotactic reaction of isopods is as follows: When the metabolism of an isopod is rapid for that individual it tends to go positive to a water current, when less rapid, negative, when still less rapid, indefinite, and when least rapid, no reaction at all is given. But a rate of metabolism that is rapid for one isopod may be slow for another, and intermediate for a third. Also an individual may give identical rheotactic responses at times when its metabolic activities measured by an absolute scale vary widely. Thus isopods kept under favorable conditions including a high oxygen tension come to have a normal mean metabolic rate and also a normal mean rheotactic response. When the metabolic rate goes above its mean the rheotactic reaction tends to become more positive; when below, less positive. Put the same isopod under similar conditions except that the oxygen tension is low and the metabolic rate is depressed and the positiveness of the rheotactic reaction also decreases. But in time the isopod becomes acclimated to the new conditions and the rheotactic reaction may go up to about its old average (table 4, isopod 12, reaction for 8/14) and plays up and down as the metabolic rate changes about its new mean. So the rheotactic reaction is an expression, not of the absolute metabolic rate of the animal but of the relative metabolic rate to which the isopod is acclimated for the time being.

SUMMARY

1. The resistance of isopods to relatively strong solutions of potassium cyanide has an inverse relation to their carbon dioxide production; the higher the rate of carbon dioxide production,

the shorter the survival time in the cyanide, hence the resistance of isopods to potassium cyanide is a fair measure of their metabolic activity (page 207).

2. The calcium ion decreases the carbon dioxide production in the isopods and renders them less positive in their rheotactic reactions (page 209).

3. There is a high degree of similarity between the variation of carbon dioxide production of individual isopods and their rheotactic reaction (page 211).

4. The rheotactic reaction is an expression of the relative metabolic activity of the animal under the conditions to which it is acclimated for the time being.

January, 1914.

LITERATURE CITED

ALLEE, W. C. 1912. An experimental analysis of the relation between physiological states and rheotaxis in Isopoda. *Jour. Exp. Zool.*, vol. 13, pp. 269-344.

1913. Further studies on physiological states and rheotaxis in Isopoda. *Ibid.*, vol. 15, pp. 257-295.

1914. Certain relations between rheotaxis and resistance to potassium cyanide in Isopoda. *Ibid.*, vol. 16, no. 3.

CHILD, C. M. 1913. Studies on the dynamics of morphogenesis and inheritance in experimental reproduction. V. The relation between resistance to depressing agents and the rate of metabolism in Planaria dorotocephala and its value as a method of investigation. *Ibid.*, vol. 14, pp. 153-206.

1913a. Certain dynamic factors in experimental reproduction and their significance for problems of reproduction and development. *Arch. Entw. Mech.*, Bd. 35, pp. 598-641.

TASHIRO, SHIRO 1913. Carbon dioxide production from nerve fibers when resting and when stimulated; a contribution to the chemical basis of irritability. *Amer. Jour. Physiol.*, vol. 32, pp. 107-136.

1913a. A new method and apparatus for the estimation of exceedingly minute quantities of carbon dioxide. *Ibid.*, vol. 32, pp. 137-145.

1914. Carbon dioxide apparatus III. Another special apparatus for the estimation of exceedingly minute quantities of carbon dioxide. *Jour. Biochem.*, vol. 16, pp. 485-494.

THE AUDITORY SENSITIVITY OF THE WHITE RAT

WALTER S. HUNTER
The University of Texas

(One Figure)

The following is a report upon some studies of the auditory sensitivity of the white rat which are in progress at the psychology laboratory of the University of Texas. In January, 1913, tests were begun upon the discrimination of noise and tone in order to ascertain whether for the rat these are sensed as different. The discrimination box was T shaped. (See figure 1.) The animal was started at the base of the T and was required to turn either to the left or to the right depending upon the stimulus given. The source of the tone was a tuning fork held in a clamp above the apparatus and actuated by striking with a rubber hammer. The fork support was mounted independent of the apparatus box so that mechanical jars could pass through the floor only, if at all. The experimenter was prepared to introduce electric tandem driven forks, but this was found unnecessary.[1]

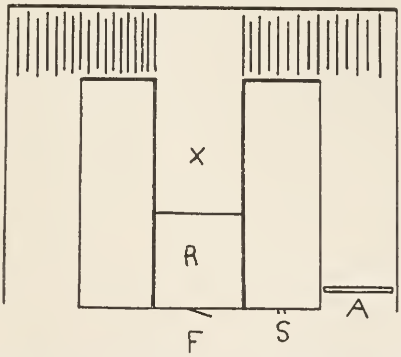


FIGURE 1. T-shaped discrimination box. F, food; R, release box; X, tuning fork was held above this point; A, alley stop, can be placed in either alley; S, switches.

---

[1] In order to make it difficult to use the thud of striking the fork as a cue, the fork was struck just as the rat was placed in the release box. In order to make the control more sure, the fork may be actuated even sooner. While in crucial cases, this method cannot supersede the tandem driven forks, in the average case it may render the use of such apparatus unnecessary.

In order to make sure that the animal got the full benefit of the stimulus, the opening of the resonance box was directed downward upon the apparatus at a height of 19 inches. The noises were given just behind and slightly above the discrimination box. Each stimulus was given from the time the rat entered the box until the food was reached behind the base of the T. Punishment and reward were used with all of the rats. Because of the noise, the inductorium was placed in a distant room of the laboratory.

The six rats of set one were required to associate a turning to the right with the tone (c′ 512 v. s.), one trial, and a turning to the left with the noise (hand clapping), a second trial. These stimuli were as nearly equal in intensity as the experimenter could secure. The intensity of the tone was approximately equal to that of a tone produced by dropping a solid rubber ball of 102 gm. upon a rigidly held c′ 512 tuning fork from a height of 100 cm. This gives a good medium intensity. In view of the rat's poor sensitivity to intensity differences in tone (see below), these measurements are only intended to give the reader a fair notion of the intensity values employed. Five trials daily were given. All six rats learned the discrimination in from 310 to 520 trials. *All of the records show a gradual decrease in the number of errors.* Controls were instituted which indicated that the auditory stimuli alone, and not extraneous cues from the experimenter or cues from the order of presentation,[2] were determining the reactions. Two series of tests were then used: (1) The tone was withheld so that the rats received at one trial a noise and at the next trial not tone, but the absence of tone.

---

[2] When the rat is confronted with a difficult discrimination, only the greatest care will prevent the "learning of the problem" on the basis of position factors. These kinaesthetic cues are often of great complexity and are influenced by punishment. The subject will repay careful study. The following types of cases, of which some have been previously described, were noted in the present tests: (1) The rat may form a habit of going always to one side. Every day he will begin in this wise: but after a series of punishments, he may change and go to the opposite side for the rest of that day. (2) A rat may alternate between sides in the order right-left. If this leads to severe punishment, he may at times reverse the alternation to a left-right order. (3) Rat No. 5 formed a habit of alternating after *each success only*. He would go to the right and, if successful, would go to the left in the next trial. Had he failed on the right, though, he would have continued to go there until he succeeded. He would then have gone to the left where the same type of performance would be again gone through.

Behavior of this nature may give the appearance of true discrimination of the stimuli presented by the experimenter. It can only be checked up by most carefully chosen variations in the order of presentations.

Result—the reactions remained at a normal accuracy. In other words, the presence of the tone was not essential for correct reactions. (2) The noise was withheld and tone given at one trial and the absence of noise at the next. Result—the rats failed. The rat always turned to the left for the noise. It turned to the right for each of the following: tone, the absence of tone, and the absence of noise.

Two interpretations[3] were now possible: (1) The rats may be unable to hear c′ 512 either because of a shortening of the scale similar to the probable shortening of the rat color spectrum, or because of an inability to hear tone at all, i. e., complete tonal deafness, or because of a tonal island. In either of the three cases, we have a sensory defect. Furthermore, it would be a defect common to all of the rats tested. (2) The ignoring of c′ 512 may be due to a factor of attention as Dr. Weidensall has pointed out in her report at the American Psychological Association. 1912.[4] Our dilemma here is the same as the one which confronted the Watsons,[5] e.g., when their rodents were shown to be ignoring red in the red-green discrimination. The solution in either case must come from evidence drawn from tests made on mere sensitivity, i.e., the discrimination of a stimulus from its absence. In view of this the following tests were made.

Three of the rats of set one, were each given 10 trials daily, in an attempt to set up an association between the tone and turning to the right and between absence of tone and turning to the left. 410, 520 and 350 trials were given, but the association was never set up. These three rats had formed the original discrimination of noise vs. tone in 310, 370 and 520 trials respectively. In all save the third rat, therefore, the original discrimination was set up in fewer trials than given in this control. I have not regarded this as entirely conclusive, however, because as a result of previous training the rats were all ignoring the tone. This habit (if habit it were) may have persisted. A new set

---

[3] There is a third possibility, viz.: the rats may have been unable to discriminate the tone from its auditory background. It was impossible to carry out the tests in a sound-proof room, so this possibilitiy has not been rigorously excluded. However, the rats were accustomed to what auditory stimuli did occur, and as far as the experimenter was concerned, the tone dominated over all other sounds save in exceptional cases that rarely occurred.

[4] Weidensall, Jean. A Critique of the Discrimination Test. *Psych. Bull.*, 1912, **9**, pp. 57–58.

[5] Watson, J. B. and Watson, Mary I. A Study of the Responses of Rodents to Monochromatic Light. *Jour. Animal Behavior*, 1913, **3**, pp. 1–14.

(II) of six untrained rats was now chosen. To this group was added one rat from set I, not included in the above three. These seven rats were given ten trials daily. Table I gives the results. Not only did these rats not learn to discriminate the tone from its absence, but the data indicate that they reacted as poorly at the close of the 700 tests as at the beginning. The objection may be made that the number of trials was insufficient ! Such a criticism I should regard as valid only if the animals were slowly improving in accuracy. This was not the case. Particular attention should be drawn to the case of Rat No. 5. This rat had learned to discriminate " noise from tone " within 400 trials. The above table shows that when tested on mere sensitivity to the tone, there was no improvement in accuracy even at the end of 700 trials.

TABLE I.

The learning processes of the rats of set 11. The numbers stand for the trials in each successive fifty that were correct.

TRIALS	RATS						
	5	13	14	15	16	17	18
50	24	26	22	19	22	22	23
100	27	17	25	22	27	27	28
150	28	24	21	17	24	24	27
200	34	26	24	24	24	28	26
250	30	24	22	25	23	30	25
300	25	24	29	26	27	25	27
350	28	23	24	23	28	26	27
400	31	23	27	21	18	22	28
450	25	26	25	22	25	24	28
500	28	23	25	27	21	25	19
550	24	19	28	24	23	22	22
600	28	23	22	25	27	25	23
650	30	24	25	23	24	28	24
700	26	21	26	25	26	24	24

The present work is of interest when compared with that of Johnson on pitch discrimination in dogs. At the present writing his complete results have not appeared; but the preliminary report[6] shows that the dogs could not discriminate between middle C and the E above. The possibility that the dogs cannot hear these tones is not considered, although the data are in harmony with such a view.

---

[6] Johnson, H. M., " Some Experiments on Pitch-Discrimination in Dogs." *Psych. Bull.*, 1912, **9**, p. 59.

Comparative psychologists are agreed, I believe, that, with the higher animals, the ability to associate a stimulus with a simple response shall be the criterion of sensitivity to that stimulus. Exceptional cases may occur, as is suggested by the studies of Yerkes upon the hearing of the frog.[7] Other factors being equal, however, where an animal can learn an association with one auditory or visual stimulus, inability to do so with another auditory or visual stimulus is to be taken as evidence of lack of sensitivity. Granting this, the above data prove either that *the rats cannot hear c′* 512, under the conditions of the present experiment, or (note 3 has some reference here) that *their sensitivity is extremely slight.* The analogies between the present conclusion and that reached by other students with respect to color vision in animals are both striking and instructive. It is to be noted in particular that tone and color correspond to periodic vibrations and that noise and the white-black series correspond in general to heterogeneous vibrations. The ability to react to periodic ether vibrations is apparently a late acquisition in animals. Why then not expect, a priori, the same to be true in sound, particularly when periodic vibrations seem to be more artificial and hence rarer (at least in the habitats of non-musical animals) than heterogeneous ones? Further comment upon this must await a later presentation of data.

In addition to the above crucial evidence on the sensitivity of the white rat to c′ 512, much other material bearing upon the same problem has been accumulated. All of this, while not in and of itself decisive, is in harmony with the conclusion above drawn.

(1) All rats of set I ignored the tone and reacted on the basis of noise and the absence of noise. There must be, then, some fundamental difference in the effect of noise and tone on the rat. Otherwise we should expect individual differences to appear.

(2) Six rats of an untrained set (III) all failed to discriminate a very intense sounding of c′ from a faint sounding of the same tone. These two intensities may be described with sufficient accuracy as follows: One was as intense as could be secured by striking the fork. The other was approximately of

---

[7] Yerkes, R. M. "The Sense of Hearing in Frogs." *Jour. Comp. Neur. and Psych.*, 1905, **15**, pp. 279-304.

the same intensity as a tone produced by a solid rubber ball of 102 gm. striking the fork after a free fall of 25 cm.

The conditions of testing here were the same as described above. Five trials daily were given, save at certain periods with two rats, with punishment and reward. Between 575 and 800 trials were given. There was no more evidence of discrimination at the last than at the first. This problem of intensity discrimination was begun simultaneously with the work on noise and tone before I suspicioned that the rats were insensitive (or very slightly so) to the tone in question.

(3) Miss Alda Barber of this laboratory is studying localization of sounds in rats. The standard stimulus, tapping upon wood, is well localized. The following controls have been used with significant results: (a) Tapping with the rubber end of a lead pencil on the resonance box of c′ is localized with normal accuracy. This gives a noise predominately of a 512 v. s. pitch. (b) A tuning fork c′ sounded steadily is completely ignored. (c) The same pitch blown upon an organ pipe as an interrupted (tooting) tone is also ignored. It is not known yet whether or not special training will overcome these last two failures.

(4) Watson[8] obtained reactions from white rats with the Galton whistle. I have never secured an *unambiguous* response to tone, although violent starts are often made to the *slightest* noises. A few times I have thought that reactions occurred. These may well have been to the noise accompanying the whistle tone. Tests have been made with organ pipes and Edelmann-Galton whistles. At least 30 rats have been tested in this laboratory both when they were awake and when they were asleep, when they were nervous and responded to slight noises readily and when they were not nervous. A few tests were made upon some twenty rats at the University of Chicago in the summer of 1913. The Edelmann whistle was used throughout its range, but no reactions were observed. Professor R. E. Carter of the University of Kansas witnessed these latter tests and agreed in the findings. Possibly it is true that rats are sensitive to each others squeaks, but who is to say whether these are more tone than noise?

This type of test is to be carried further. At present this method of "general response" has convinced me more strongly merely that there is a fundamental difference for the rat in noise and tone.

---

[8] Watson, Jno. B. "Kinaesthetic and Organic Sensations." *Psych. Rev. Mon.*, 1907, 8, pp. 53-54.

(5) It will be recalled that only three rats of set I were tested immediately upon sensitivity to tone vs. no-tone. The other three rats were tested as follows: In place of hand claps, the following noises were each substituted for five trials from time to time: (a) rattling of paper; (b) dropping sunflower seed on tin; (c) scratching on wood; (d) drumming on the table with the fingers; (e) rubbing two pieces of board together; (f) hissing through the teeth; and (g) rattling of nails in a glass. Pitch, volume and quality varied greatly, but a rough attempt was made to keep the intensity values equal to that of the tone. (See above, page 216.) *The rats responded to all of these stimuli as accurately as to the regular stimulus of hand claps*, i.e., never below 80% correct. Rat No. 5 failed to react correctly to noises e and f, i.e., although repeatedly tested, he never made more than from 55% to (at most) 70% correct. This was the rat tested later with set II, on tone vs. no-tone, with negative results. In view of those tests, his failure to respond correctly to the two noises is to be explained on the basis of their dissimilarity to the standard noise rather than upon their likeness to c′ 512, which tone this rat seems not to hear.

Tests were also made in which each of the following tones were substituted for the original c′ on the fork on enough occasions to be sure that the reactions were not due to chance: (1) c‴ 2048 on the fork; (2) c′ 512 v. s. on the organ pipe, sounded steadily; (3) No. 2, sounded interruptedly, i.e., in toots; (4) c″ 1024 on the organ pipe, sounded steadily; (5) No. 4 sounded interruptedly; and (6) f 341.3 on the organ pipe, sounded steadily. With *no exception*, the rats reacted to these tonal stimuli as to the original tone which had been sounded steadily, i.e., they ignored them. There are many suggestions as to interpretation which arise from these results. The points that can be definitely stated are these: (1) All of the tones given were for some reason very different from the noises. (2) This difference was not the fact of smoothness, i.e., lack of interruptedness. This point seems conclusively proved, because on the same day with the interrupted noises were given trials with the interrupted tones, yet the rats paid no more attention to the tones than if they had been continuously sounded. Inasmuch as the animals reacted in the same manner to all of the noises, it is certainly a striking fact that none of the tonal stimuli given were classed as noises. Further experimentation alone will determine whether sensory defect is the reason for neglecting all of the tones given here. Such an explanation certainly seems necessary for the lack of sensitivity to c′ 512.[9]

At the present, the above work is being extended in three directions: (1) Search is being made throughout the pitch scale for a tone to which the rats will respond. Both continuous and interrupted tones will be used. When an effective tone is found, the original problem will again confront us, viz., can rats hear noise and tone as distinct experiences. (2) Miss Barber's work will probably throw added light upon the question of relative sensitivity to noise and tone. (3) Mr. A. C. Scott is beginning tests which are expected to emphasize the relations between vision and hearing with respect to the learning processes involved. One problem with which he will deal will be this: Is the simultaneous presentation of stimuli, such as is used in visual discrimination, more favorable to learning than a successive presentation of stimuli, such as must be used in auditory discrimination work?

One additional matter needs comment. So far as I have been able to ascertain there are no published studies on the anatomy of the white rat's ear. I am supported in this statement by several eminent authorities. In view of the results above presented, it is at least possible that careful anatomical studies might throw light upon the structural basis for the perception of noise and tone.

---

[9] Johnson's work[10] has appeared since this paper went to press. On pp. 44–45, the author reports negative results at the conclusion of 150 trials on mere sensitivity to a tuning fork of 256 d. v. The suggestion is made from this that in ordinary noises the dog may reach only to high overtones.

[10] Johnson, H. M. Audition and Habit Formation in the Dog. Behavior Monographs, **2**, no. 3, 1912.

BEHAVIOR OF THE MEDITERRANEAN FRUIT FLY (*CERATITIS CAPITATA* WIED.) TOWARDS KEROSENE

HENRY H. P. SEVERIN, PH.D. AND HARRY C. SEVERIN, M.A.

The following observations on the behavior of the Mediterranean fruit fly toward kerosene were made in the field in Manoa Valley, situated on the outskirts of the city of Honolulu, Hawaii. On account of the abundance of rainfall in this valley, the kerosene traps used in our experiments consisted of pans three and one-half inches in depth and twelve inches in diameter. Each pan was wired to the lower branches of a fruit tree (Fig. 1).

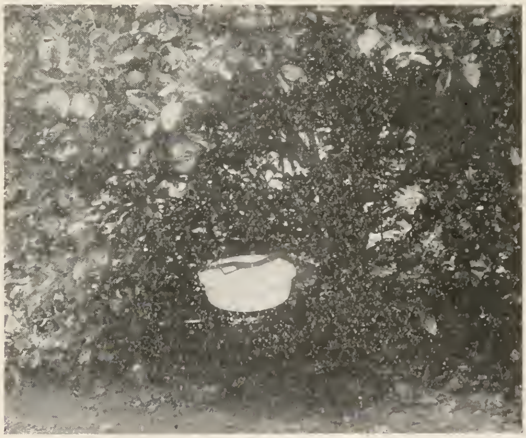


FIGURE 1. Pan containing kerosene wired to the lower branches of a fruit tree, to trap the Mediterranean fruit fly.

Enough kerosene was poured into each pan to cover the bottom so that in case of a heavy rain, the kerosene might overflow directly to the ground and not injure the tree. After a light or moderate rain such traps are probably just as effective as when there is no precipitation, for the oil floats on the surface of the water.

The first problem which presented itself was to determine whether the color of the pan containing the kerosene made any difference in the number of Mediterranean fruit flies caught. Five white, three black, one blue and seven orange-colored pans were wired to the branches of orange, lemon, grapefruit and guava trees. From the results of our catches in the various pans, it was evident that the number of fruit flies captured was not influenced by the color of the pans. Moreover, it is highly probable that the sense of smell is the determining factor in attracting these insects to the kerosene.

In our second experiment we endeavored to ascertain in what particular kind of fruit-bearing tree of an orchard the pest would be captured in largest numbers with the kerosene traps. Accordingly, one pan was wired to the lower branches of a common guave tree (Psidium guayava pomiferum), nine pans were fastened in nine different navel orange trees (Citrus aurantium), and one pan was placed in a Java plum tree (Syzygium jambolana). All of the pans used in this experiment were enameled white, because most insects caught in the oil were more conspicuous against such a background. The following table shows the number of fruit flies taken at intervals of three to four days for a period of eighteen days in the kerosene traps attached to the three different kinds of fruit trees:

TABLE 1

NUMBER OF MEDITERRANEAN FRUIT FLIES CAPTURED IN KEROSENE TRAPS PLACED IN GUAVA, ORANGE AND PLUM TREES.

	Trees		
	One guava	Nine navel orange	One Java plum
Four days catch..............	75	1155	398
Four days catch..............	33	749	207
Three days catch.............	25	715	213
Three days catch.............	16	422	60
Four days catch..............	35	1093	295
Eighteen days catch..........	184	4134	1173
Average capture per day in 1 trap....................	10	25	65
Total number of males captured......................			5461
Total number of females captured....................			30
			5491

It is evident from this table that the attraction of the Mediterranean fruit fly to the kerosene was confined almost entirely to the male sex. Female flies were present in this orchard because hundreds were caught by sweeping with an insect net among the fruit trees. Trapping the pest with kerosene was carried on for a period of eight months in the Hawaiian Islands in connection with other experiments and the results show that of every one thousand fruit flies captured only three on an average were females, the remainder being males.

A dissection of some of the flies captured in the kerosene trap wired to the Java plum tree showed that the alimentary canal was filled with the blue juices of the plum. The ripe plums were seriously infested by the maggots of different species of Drosophilidae and the juices were exuding from the punctured and bruised fruit. Mediterranean fruit flies and some of these plums were placed in a breeding jar and frequently the Trypetids were seen feeding on the plum juices. The reason why more specimens were captured in the kerosene trap wired to the Java plum tree finds its probable explanation in the fact that the plum is more attractive to the pest then the common guava or navel orange, or possibly because the plum juice was more available than the juices of the less bruised guavas and oranges.

The Mediterranean fruit fly was often captured in kerosene traps wired to trees that were not bearing fruit and also near fruits in which the pest has not been reported to breed. Kerosene traps were fastened repeatedly in mango trees (Mangifera indica) months before the mango season was on, and in every instance fruit flies were trapped. One trap was wired in an isolated bread fruit tree (Artocarpus incisa) which at that time bore very hard, green fruit, and in four days twenty-nine male Mediterranean fruit flies were caught. A kerosene trap was also placed in a clump of mulberry shrubs (Morus nigra) bearing ripe fruit, and in four days twelve male flies were taken. In the last catch the flies may have been attracted by the ripe fruit, the juices probably serving as food material for the adults. The interesting part of the last two catches rests in the fact that the pest under consideration does not breed in the fruits of these trees.

In all probability the reaction of the male Mediterranean fruit fly to kerosene is not in any way connected with the feeding habits, but too much emphasis, however, should not be attributed to any of these experiments, for the distance that kerosene will attract the flies is not known.

Weinland (2, page 847) claims that the sphere of influence of kerosene " is limited, being possibly fifty feet or so, varying with the wind, freshness of kerosene, etc." Howlett (1, page 414) of India says the distance at which the fruit flies (Dacus zonatus Saund.) are able to perceive the smell of citronella oil "is doubtful, but seems to be considerable; half a mile is probably not extravagant an estimate if the wind is favorable."

The behavior of the Mediterranean fruit flies was occasionally observed in the neighborhood of the kerosene traps. In some instances fruit flies remained at rest on the inside of the pans for long periods of time as if stupefied by the volatile parts of the oil. In other cases, the flies would walk along the inside of the pan for a time, then take wing and fly up to a neighboring leaf or twig, or in their apparently dizzy, zigzag flight over the surface of the oil they would plunge into the kerosene and generally cease all activity noticeable to the naked eye in less than half a minute.

It certainly is peculiar that the Mediterranean fruit fly plunges into the kerosene to its own destruction. The flies may be attracted to the oil as a result of a chemotaxis due to one or more hydro-carbons or to the impurities of the petroleum oils, such as the sulphur constituents or nitrogenous products. Small quantities of sulphides are detected by the human nose and it may be possible that the minutest traces are perceived by the fruit flies. Furthermore, sulphides have recently been found within the bodies of insects. Again, the hydro-carbons of the oil may act as an anesthetic, and stupefy the insects whenever they remain within its influence. It is known that the volatile parts of gasoline, for instance, have a stupefying effect upon animals. According to a scientist connected with the Standard Oil Company, cases are on record where men, who had opened barrels of gasoline, were suddenly overcome by the fumes and plunged "head-first" into the oil. Large gasoline tanks which have been recently emptied are dangerous for men to go into, and require about twenty-four hours of ventilation before they are safe for a human being to enter.

Why should enormous numbers of male fruit flies and only a few females be captured in certain oils? Concerning the behavior of Dacus zonatus towards citronella oil, Howlett (1, page 413) writes: " Since the reaction was confined to the male sex and did not appear to be in any way connected with feeding habits, it seemed most reasonable to suppose that the smell might resemble some sexual odour of the female which in natural conditions served to guide the male to her." This is, in substance, a view which we also expressed to a number of entomologists and mentioned in a paper read before the Agricultural Seminar in Honolulu on January 11, 1912, to explain the behavior of the male Mediterranean fruit fly towards kerosene. Howlett believes that "the smell is in all probability perceived by means of the antennae," for, after he had carefully amputated these "at the base of the second joint," none of the mutilated insects were attracted to the oil of citronella.

If it is true that kerosene gives off an odor which resembles that emitted by the female fruit flies to attract the opposite sex, then how would the fact be explained that a few females are usually caught in the oil? We would have to assume that the specialized sense organs present in the males to locate the females are absent in the latter. We would then be forced to conclude that the females were not attracted to the kerosene, but came within the sphere of influence of the oil by accident, became stupified and dropped into the oil. There is, of course, the possibility that the reaction of the male Mediterranean fruit fly towards some volatile part of the petroleum oils may be a positive chemotaxis "not representing the sexual smell of the female," a possibility to which Howlett also calls attention in the behavior of Dacus zonatus toward citronella oil.

BIBLIOGRAPHY

1. Howlett, F. H. The Effect of Oil of Citronella on Two Species of Dacus. 1912. *Trans. Ent. Soc. London*, pt. II, pp. 412-8.
2. Weinland, H. A. The Present Fruit Fly Situation and some Results of the 1912. Hawaiian Campaign. *Cal. State Comm. Hort.*, Mon. Bull. I, No. 11, pp. 845-852.

JOURNAL OF ANIMAL BEHAVIOR

VOL. 4 JULY-AUGUST, 1914 No. 4

THE FACTORS DETERMINING THE VERTICAL MOVEMENTS OF *DAPHNIA*

LEE RAYMOND DICE

From the Zoölogical Laboratory of the University of California

CONTENTS

PAGE
Introduction.
Part I. Experimental 231
  Phototaxis in Relation to:
    Light Intensity 231
    Temperature 235
    Chemical Content of Water 236
    Mechanical Stimulation 236
    Time of Day 237
  Geotaxis in Relation to:
    Light Intensity 237
    Temperature 242
    Chemical Content of Water 244
    Mechanical Stimulation 245
    Time of Day 245
  Locomotor Activity in Relation to:
    Light Intensity 245
    Temperature 246
    Chemical Content of Water 248
    Mechanical Stimulation 248
    Time of Day 249
  Thermotaxis 249
  Chemotaxis 249
  Pressure 249
Part II. Discussion 250
  Observed Vertical Movements in *Daphnia* 250
  Vertical Movements Caused by:
    Changes in Light Intensity 253
    Changes in Temperature 255
    Mechanical Stimulation 257
    Changes in Chemical Content of the Water 258
    Aging of Individuals 258
  General Features of Behavior in *Daphnia* 259
  Reversal of Geotaxis in other Plankton Animals 262
  Summary 263
  Literature 264

INTRODUCTION

Vertical movements of the plankton crustacea have been noted by many observers. The published results show that there is great variation in the movements made by different species, and that the same species in different lakes shows great differences in its vertical migrations. These facts indicate that there is a considerable number of factors which operate together to determine the movements. This paper is presented with the hope that it will help to make clear the relative importance of the factors determining the movements of a common fresh water entomostracean.

This study has been carried on under the direction of Dr. S. J. Holmes to whom the author is indebted for constant advice and criticism. To Professor E. P. Lewis of the Department of Physics thanks are due for information concerning the absorption of ultra-violet rays in passing through the atmosphere and through water. Dr. A. C. Chandler assisted in taking observations in some of the longer experiments.

In the following experiments only one species of crustacean was used, *Daphnia pulex* De Geer, which was found abundantly at times in the lakes and ponds about Berkeley. The specimens used were obtained from several artificial ponds on the University Campus. Many were kept for some time in glass aquaria in the laboratory before being used for experimentation in order to accustom them to laboratory conditions; others were used immediately after being collected from the pond in order to ascertain how far the behavior had been modified by the artificial conditions. It has been observed that daphnids in different stages of their life history show differences in their vertical movements. To avoid this complication only adult individuals were used.

In all these experiments the animals were kept in water taken from the same aquarium as the animals unless a statement is made to the contrary. In the experiments on geotaxis the jars were filled completely and the top sealed by a ground glass stopper to exclude the possibility of a difference of oxygen content between the top and the bottom. To avoid the possibility of chance in the animals remaining constantly at one end or the other of the dish, the ends were occasionally reversed or the contents of the dish stirred up.

The experiments were performed between August, 1913 and April, 1914 in the Zoological Laboratories of the University of California at Berkeley.

PART I. EXPERIMENTAL

PHOTOTAXIS IN RELATION TO LIGHT INTENSITY

The individuals of *Daphnia pulex* are normally positively phototactic and under conditions similar to those they would meet in nature it is difficult to obtain from them a negative response. In weak light or moderately strong light most of them are strongly positive. To the light from a 100 watt Mazda lamp at a distance of 30 centimeters they remained strongly positive throughout an exposure of nearly six hours. (Exp. 1.)

Exp. 1

Phototaxis in weak light

January 29, 8.30 A.M., 18 *Daphnia pulex* from diffuse daylight placed in a glass dish 28 cm. long marked off into five transverse divisions. Exposed in darkroom to horizontal light from 100 watt Mazda lamp at 30 cm. Temperature 17.5° C.

Divisions	Positive end I	II	III	IV	Negative end V
9.00 A.M.	*14	1	1	2	0
9.15	15	1	0	1	1
9.45	15	1	0	2	0
10.50	15	1	0	2	0
11.50	15	2	0	0	1
1.00 P.M.	14	0	1	0	3
2.00	13	3	0	1	1
2.20	13	2	1	2	0
Averages	14.2	1.4	0.4	1.2	0.8

Another experiment (Exp. 2) shows that to the weak light from a 50 watt Edison lamp at 50 centimeters the animals remain positive during a continuous exposure of 60 hours. Probably they would remain positive indefinitely to these intensities. It appears that they are more strongly positive in the stronger light.

---

* The figures refer to the number of individuals in each division.

Exp. 2

Phototaxis in weak light

March 23, 4 P.M., 25 *Daphnia pulex* placed in a 28 cm. long glass dish marked off into five divisions. Exposed in darkroom to horizontal light from a 50 watt Edison lamp at 50 cm. distance. Temperature 17.5° C.

Divisions	Positive end I	II	III	IV	Negative end V
Mar. 24, 4 P.M.	20	0	1	1	3
8	17	2	2	2	2
12	14	1	5	2	3
Mar. 25, 4 A.M.	10	2	3	5	5
8	13	1	5	4	2
12 M.	14	1	3	2	5
4 P.M.	10	3	5	4	3
8	10	2	6	3	4
Mar. 26, 8 A.M.	13	5	1	1	5
Averages	13.4	1.9	3.4	2.7	3.5

These daphnids, at temperatures of 20° to 23° C., are generally nearly neutral to diffuse daylight (Exp. 3), to the light from a 15 ampere electric arc (Exp. 4), or to sunlight lacking the ultra-violet rays (Exp. 5). Experiment 3 shows a rather large variation in the distribution of the animals during the experiment which is probably due to the changes in light intensity corresponding to changes in the position of the sun.

Exp. 3

Phototaxis in diffuse daylight

March 19, 8 A.M., 22 *Daphnia pulex* from laboratory aquarium placed in a 28 cm. long glass dish marked off into three divisions. Exposed to diffuse light from a south window covered by a white screen. Light rays from the room were excluded by a black lined box. Temperature 23° C.

Divisions	Positive end I	II	Negative end III
8.20 A.M.	6	5	11
8.45	6	6	10
9.30	9	3	10
10.00	8	3	11
11.00	8	7	7
12.00 M.	9	8	5
1.00 P.M.	9	6	7
2.00	9	7	6
3.00	9	8	5
4.00	11	7	4
5.00	10	9	3
6.00	13	6	3
Averages	8.9	6.3	6.8

Exp. 4

Phototaxis in arc light

January 29, 18 *Daphnia pulex* which had been exposed to the light of a 100 watt Mazda lamp for four hours were placed in a glass dish 28 c.m long marked off into five divisions. Exposed them to the horizontal light from a 15 ampere electric arc at a distance of 40 cm. The light was passed through 8 cm. of water to cut out the heat.

	Positive end				Negative end
Divisions	I	II	III	IV	V
2.30 P.M.	7	1	1	1	8
2.40	7	2	2	2	5
2.50	6	0	1	3	8
3.00	8	1	3	0	6
3.10	7	1	3	2	5
3.20	5	2	3	2	6
3.30	4	0	6	2	6
4.00	9	3	2	1	3
4.30	2	1	3	4	8
5.25	8	1	2	2	5
Averages	6.3	1.2	2.6	1.9	6.0

Exp. 5

Phototaxis in sunlight

April 13, 2 P.M., 13 *Daphnia pulex* from laboratory aquarium placed in 18 cm-long glass dish marked off into five divisions. Exposed to sunlight with ultra. violet rays cut off by one sheet of window glass. Temperature kept at 21° to 22° C.

	Positive end				Negative end
Divisions	I	II	III	IV	V
2.05 P.M.	4	1	2	4	2
2.15	2	1	4	2	4
2.20	1	2	2	2	6
2.25	3	3	2	1	4
2.30	1	2	3	3	3
2.50	2	4	2	1	4
3.30	5	1	2	2	4
3.40	4	3	0	1	5
3.50	7	2	1	0	3
4.00	8	1	2	1	1
Averages	3.7	2.0	2.0	1.7	3.6

In these experiments it is shown that at temperatures of from 17° to 22° C. these daphnids are normally positive to weak electric light or to moderately strong light. They are more strongly positive to moderately strong light than to very weak light. The positive phototaxis to weak light persists for seemingly indefinite periods. To light intensities stronger than weak diffuse daylight these animals are indifferent and do not become negatively phototactic to any intensity of ordinary light at these temperatures.

It has been shown by Moore (1912) that *Daphnia pulex* may be made negatively phototactic by the ultra-violet rays from a mercury vapor arc lamp. The ultra-violet rays in sunlight are nearly all absorbed in passing through the atmosphere. However, experiment 6 indicates that the quantity of these rays reaching the surface of the earth at sea level (altitude of Berkeley about 100 feet) is sufficient to have a slight effect in causing negative phototaxis. In passing down through the water of a lake the ultra-violet rays will be very rapidly absorbed. In lakes at high altitudes, which receive more of these rays than lakes at sea level, and in lakes whose water is very clear the effects the negative phototaxis caused by these rays in the bright part of the day might operate to keep the daphnids down a short distance from the surface.

Exp. 6

Effect of ultra-violet rays on phototaxis

April 13, 2 P.M., 13 *Daphnia pulex* from laboratory aquarium placed in an 18 cm. long glass dish marked off into five divisions. Temperature 21° to 22° C. Exposed to sunlight with the ultra-violet rays cut off by one thickness of window glass.

	Positive end				Negative end
Divisions	I	II	III	IV	V
2.05 P.M.	4	1	2	4	2
2.15	2	1	4	2	4
2.25	3	3	2	1	4
2.50	2	4	2	1	4
Removed window glass					
2.51	2	1	0	0	10
2.52	0	0	0	6	7
2.53	2	0	2	3	6
2.55	2	0	2	2	7
3.10	2	0	0	4	7
3.20	3	0	2	4	4
Replaced window glass					
3.25	4	2	2	2	3
3.30	5	1	1	2	4
Averages without ultra-violet rays:	3.3	2.0	2.2	2.0	3.5
Averages with ultra-violet rays:	1.8	0.2	1.0	3.2	6.8

Frisch and Kupelweiser (1913) state that after a short exposure *Daphnia magna* and less evidently *Daphnia pulex* become indifferent to the light and show no decided phototaxis so long as the intensity remains the same. When the light intensity is decreased the animals become temporarily positive while on increase of intensity they become temporarily negative. After a few minutes exposure to a new intensity the daphnids again become indifferent to the light and uniformly distributed throughout the dish. It has been shown above that in weak light or in light of moderate intensity *Daphnia pulex* remains constantly positive. Within the range of these intensities I have been unable to reverse even temporarily the phototaxis by sudden change of intensity. However, within the limits where the light intensity is strong enough so that the daphnids are normally indifferent, sudden changes of intensity produce the effects noted by the above mentioned authors. The tendency to these effects is probably present on any sudden change of intensity, but in weak light this tendency is overpowered by the normal phototaxis. It does not seem likely that these temporary changes of phototaxis can be of much importance in causing the vertical migrations of *Daphnia*.

PHOTOTAXIS IN RELATION TO TEMPERATURE

Loeb (1906) found that daphnids which were indifferent to light at 19° C. became positive when the temperature was reduced to 11° C. When the temperature was raised to 25° C. they became again indifferent or weakly negative. My experiments show the same results. Daphnids indifferent to sunlight at 20° C. show positive phototaxis to the same light at low temperatures. This first becomes pronounced at about 12° C. Animals positive to diffuse light showed a slight reduction of the positive phototaxis on heating to 32° C.

In diffuse light to which *Daphnia pulex* was positive at 22° C. Yerkes (1900) found no change of phototaxis on raising the temperature, although this was carried to the point where all the daphnids died. In weak or moderately weak electric light I have been unable to detect a variation in phototaxis on any amount of heating. We may then conclude that decrease of temperature causes a tendency to increase of positive phototaxis while increase of temperature causes a tendency to decrease of positive phototaxis, but that in weak light these tendencies are overpowered by the normal positive phototaxis.

The temperature at which these animals become indifferent to light varies with the light intensity. Below 15° C. they seem to be positive in any intensity. To weak light they seem positive at all temperatures. Above 25° C. in very strong light there may be a slight negative phototaxis, but if the ultra-violet rays are screened off this seems never to be at all strong.

PHOTOTAXIS IN RELATION TO THE CHEMICAL CONTENT OF THE WATER

Oxygen: No observable change in phototaxis was produced by changing daphnids from tap water containing much oxygen to the same kind of water from which the oxygen had been driven off by boiling for a half hour, or by the reverse change.

Carbon dioxide: Loeb (1906) has found that carbon dioxide will make neutral daphnids positive to light. Moore (1912) has further shown that this substance will make negative daphnids positive. This chemical then has a tendency to render *Daphnid pulex* positively phototactic.

Food: No observations are at hand bearing on the effect of food substances on phototaxis.

Waste products: A very large number of daphnids were placed in a small vessel and exposed to weak light. They remained positive to this light until the excess of organic waste products in the medium grew so great that all died.

The tendency of carbon dioxide to produce positive phototaxis seems to be the only factor in the relationship between the chemical content of the water and phototaxis that is likely to be of importance in the normal movements of *Daphnia*.

PHOTOTAXIS IN RELATION TO MECHANICAL STIMULATION

Yerkes (1900) states that some individuals of *Daphnia pulex* may be made temporarily weakly negative to light by mechanical stimulation, such as picking them up in a pipette, but with many individuals he failed to obtain this result. I have been unable to produce negative phototaxis by any amount of gentle or rough handling, either by picking the animals up in a pipette or by shaking the dish.

PHOTOTAXIS IN RELATION TO TIME OF DAY

Daphnids exposed in the darkroom to weak horizontal light from a 50 watt Edison lamp at 50 cm. distance, with observations taken each hour for 30 hours, gave no evidence of a change in phototaxis corresponding in any way to a daily period. Neither could such a change be detected in daphnids exposed for 24 hours to the same weak light before beginning the series of observations. In no experiment is there found the least evidence for believing in the existence of any sort of a rhythm in phototaxis independent of the direct effect of recurrent external changes.

GEOTAXIS IN RELATION TO LIGHT INTENSITY

When daphnids which have been kept some time in darkness are suddenly exposed to light of any intensity coming from a horizontal direction there is a tendency for them to go to the bottom of the dish (Exp. 7). Conversely, when daphnids which have been exposed to light of any intensity are placed in complete darkness they show a tendency to rise to the top of the dish. A tendency to positive geotaxis is also found on changing from weak light to stronger light (Exp. 8), or from moderately strong light to the light from an electric arc (Exp. 9). There is also a tendency of this kind on changing from shade to sunlight (Exp. 10). Negative geotaxis is produced by the reverse change in each of these cases.

Exp. 7

Effect of change of light intensity on geotaxis

March 18, 11 A.M., 14 *Daphnia pulex* from 17 hours in darkness placed in a 14 cm. high glass jar marked off into three divisions. Cooled to 13° C.

	Top		Bottom
Divisions	I	II	III
11.15 A.M.	8	1	5
11.30	9	0	5
11.45	8	1	5
11.50	5	2	7
Turned on light of a 40 watt Edison lamp at a horizontal distance of one meter.			
11.51	2	2	10
11.52	0	2	12
11.53	0	1	13
11.54	0	0	14
11.55	0	0	14
Light turned off.			
12.00	7	0	7
Averages in darkness:	7.4	0.8	5.8
Averages in light:	0.4	1.0	12.6

Exp. 8

Effect of change of light intensity on geotaxis

January 20, 2.30 P.M., 11 *Daphnia pulex* from diffuse light of laboratory placed in a 29 cm. high jar marked off into five divisions. Top sealed. For weak light used horizontal light from a 40 watt Edison lamp at 2 meters, and for strong light used a 100 watt Mazda lamp at a horizontal distance of 20 cm.

Divisions	Top I	II	III	IV	Bottom V
		Weak light			
2.45 P.M.	1	3	4	1	2
2.50	2	2	2	2	3
2.55	3	2	2	2	2
		Strong light			
3.00	0	0	0	0	11
3.05	0	2	0	1	8
3.10	1	1	1	2	6
3.15	1	0	2	0	8
3.20	1	2	1	3	4
3.25	1	2	1	1	6
3.45	0	1	1	1	8
		Weak light			
3.55	7	1	2	0	1
4.00	9	1	2	0	1
4.10	6	2	1	1	1
4.20	7	2	0	0	2
4.45	5	3	0	0	3
		Strong light			
4.50	0	0	0	0	11
4.55	1	0	0	1	9
5.00	2	2	0	0	7
		Weak light			
5.05	8	1	0	1	1
5.10	10	0	0	0	1
		Strong light			
5.11	0	0	0	0	11
5.15	2	1	1	1	6
		Weak light			
5.20	10	0	0	0	1
		Strong light			
5.21	2	1	1	0	7
5.25	5	0	0	1	5
		Weak light			
5.30	10	0	0	0	1
5.40	8	0	0	1	2
5.50	8	0	0	0	3
		Strong light			
5.55	1	0	1	1	8
6.00	2	0	1	0	8
Average in weak light:	6.7	1.1	0.9	0.5	1.8
Average in strong light:	1.2	0.8	0.6	0.8	7.7

Exp. 9

Effect of change of light intensity on geotaxis

January 29, 2 P.M., 50 *Daphnia pulex* collected from pond and placed in a 29 cm. high jar marked off into five divisions. Top sealed. For strong light used a 15 ampere electric arc at 40 cm. and for weak light used a 100 watt Mazda lamp at 40 cm. The light was horizontal in each case and was passed through 8 cm. of water to cut out the heat.

	Top				Bottom
Divisions	I	II	III	IV	V
3.11 P.M.	Strong light turned on.				
3.14	1	2	6	10	31
3.24	2	4	5	12	27
3.29	4	3	10	10	23
3.44	1	2	5	10	32
3.54	2	3	4	10	31
4.04	0	3	5	10	32
4.24	2	2	3	10	33
4.44	1	3	5	8	33
4.49	1	4	7	10	28
		Weak light			
4.54	24	10	5	4	7
4.59	21	10	4	7	8
		Strong light			
5.04	1	3	2	8	36
5.14	2	1	5	8	34
5.24	1	1	4	10	34
Averages in strong light:	1.5	2.6	5.1	9.7	31.1
Averages in weak light:	22.5	10.0	4.5	5.5	7.5

Exp. 10

Effect of change of light intensity on geotaxis

March 26, 17 *Daphnia pulex* in diffuse light of laboratory placed in 29 cm. high jar marked off into five divisions. Cooled to 13° C.

	Top				Bottom
Divisions	I	II	III	IV	V
9.10 A.M.	4	2	1	1	9
9.11	Exposed to sunlight. Jar inclined at right angles to the rays.				
9.12	0	0	0	1	16
9.13	0	0	0	0	17
		Placed in shade			
9.14	0	0	0	1	16
9.15	0	1	4	1	11
9.16	3	1	1	1	11
9.20	4	0	1	4	8
Averages in shade:	2.2	0.8	1.4	1.6	11.0
Averages in sunlight:	0.0	0.0	0.0	0.5	16.5

The tendency to go to the bottom on increase of light intensity cannot be due to a decrease of locomotor activity as it has been shown by Yerkes (1900) that the locomotor activity increases with increase of light intensity. Neither can it be due to a change of phototaxis because it takes place when the light comes from a horizontal direction. Further, it can be observed that following a great increase of light intensity many of the animals swim directly downwards with the head pointed toward the bottom of the dish. It seems that we have to do here with a change of some sort in the orientation of the animals to the force of gravity. The tendency to move upward following a decrease of intensity is also well marked and must also be due to a change in the reaction of the animals to gravity.

Exp. 11

Independence of geotaxis caused by change of light intensity from phototaxis

February 19, 8.15 A.M., 18 *Daphnia pulex* from 14 hours in darkness placed in a 29 cm. high jar marked off into five divisions. Exposed to the horizontal light from a 15 ampere electric arc at 50 cm. distance.

	Top				Bottom
Divisions	I	II	III	IV	V
8.46 A.M.	0	0	0	0	18
8.47	0	0	2	8	8
8.50	0	0	1	3	14
Arc moved to a position above at an angle of 45 degrees					
8.56	0	0	0	1	17
9.00	0	2	2	5	9
9.02	0	0	1	4	13
9.05	0	0	1	5	12
Arc moved back to horizontal position					
9.15	0	0	0	1	17
9.20	0	0	0	2	16
Arc below at angle of 45 degrees					
9.25	0	4	3	2	9
9.30	0	3	3	4	8
9.35	1	1	4	6	6
9.40	0	2	5	4	7
Arc back to horizontal position					
9.45	0	0	3	3	12
10.00	0	2	1	3	12
10.45	0	2	2	2	12
Arc off. On light of 40 watt Edison at 50 cm. horizontal					
10.50	1	4	5	1	7
11.00	5	4	1	2	6
11.15	5	7	3	1	2
11.25	9	2	1	1	5

Proof that the reversal of geotaxis by changes in light intensity is independent of phototaxis is given in Experiment 11. Here the daphnids remained at the bottom of the dish when exposed to the light from an arc light, no matter whether the light was falling from the side or at an angle of 45 degrees from above or below. When exposed to weak light following the exposure to the arclight the daphnids showed a strong upward tendency indicating that the effect on geotaxis in this case was undoubtedly due to the light intensity.

Experiment 12 is presented to show that the vertical distribution remains altered for a long time after reduction of light intensity.

Exp. 12

Persistence of negative geotaxis in darkness

March 28, 8.30 A.M., 10 *Daphnia pulex* from laboratory aquarium at a temperature of 18.5° C. placed in a 29 cm. high jar marked off into five divisions. Exposed to diffuse light of laboratory. Cooled to 13° C.

	Top				Bottom
Divisions	I	II	III	IV	V
9.30 A.M.	1	1	2	2	4
10.00	1	5	0	0	4
10.30	0	1	2	3	4
11.00	3	2	2	0	3
		Placed in darkness			
11.30	6	1	0	0	3
12.00 M.	5	2	1	0	2
1.00 P.M.	3	2	0	2	3
2.00	4	1	1	1	3
3.00	5	1	1	0	3
4.00	6	1	0	1	2
Averages in light at 13° C.:					
	1.2	2.3	1.5	1.2	3.8
Averages in darkness at 13° C.:					
	4.8	1.3	0.5	0.7	2.7

We have shown that in *Daphnia pulex* increase of light intensity causes a tendency toward positive geotaxis, while decrease of intensity causes a tendency toward negative geotaxis. This tendency seems to be stronger the greater the change in intensity. It seems also that these tendencies are persistent for a considerable length of time.

GEOTAXIS IN RELATION TO TEMPERATURE

On heating *Daphnia pulex* in the dark to a temperature of about 25° C. there is a strong tendency for the animals to go to the bottom of the dish (Exp. 13). On cooling them to a temperature of about 15° C. there is a tendency for them to go to the surface (Exp. 14). The position of these animals kept in the dark was determined by turning on a weak light and taking the observation before the position of the animals could change. The tendency to go down on heating cannot be due to the effect of temperature on the locomotor activity, because it will be shown in a later section that increase of temperature causes an increase of locomotor activity which would tend to cause the animals to move upwards. Neither can this tendency be due to any effect of light because the tendency is present in the complete absence of light. Seemingly it is due to a change in the orientation of the animals with respect to gravity. We may then suppose that the tendency to move upward on cooling is also due to a change in the relation of the animals to the force of gravity. In horizontal light the same effect of temperature on geotaxis is found (Exp. 15).

Exp. 13

Positive geotaxis caused by heating

March 19, 8 A.M., 10 *Daphnia pulex* from 14 hours in darkness placed in a 29 cm. high jar marked off into three divisions. Kept in complete darkness except when making observations. Temperature 21° C.

	Top		Bottom
Divisions	I	II	III
8.15 A.M.	4	4	2
8.45	1	2	7
	Heated to 26° C.		
9.00	2	0	8
9.30	0	0	10
10.00	0	2	8
11.00	0	3	7
12.00 M.	0	1	9
1.00 P.M.	1	2	7
2.00	1	1	8
3.00	0	1	9
4.00	0	2	8
5.00	0	0	10
6.00	1	1	8
Averages at 21° C.:	2.5	3.0	4.5
Averages at 26° C.:	0.5	1.2	8.3

Exp. 14

Effect of temperature on geotaxis

March 19, 8 A.M., 10 *Daphnia pulex* kept 14 hours in darkness placed in a 29 cm. high jar marked off into three divisions. Still in complete darkness. Temperature 21° C.

	Top		Bottom
Divisions	I	II	III
8.15 A.M.	2	1	7
8.45	1	1	8
	Cooled to 13° C.		
9.00	6	0	4
9.30	3	0	7
10.00	3	1	6
11.00	5	1	4
12.00 M.	6	0	4
1.00 P.M.	4	3	3
2.00	6	0	4
3.00	4	2	4
4.00	3	0	7
5.00	3	0	7
6.00	3	0	7
Averages at 21° C.:	1.5	1.0	7.5
Averages at 13° C.:	4.2	0.6	5.2

Exp. 15

Effect on geotaxis of change in temperature

February 26, 15 *Daphnia pulex* 15 hours in darkroom exposed to horizontal light from an 80 watt Edison lamp at 2 meters placed in a 29 cm. high jar marked off into five divisions. Experiment in same light.

	Top				Bottom	
Divisions	I	II	III	IV	V	
8.55 A.M.	4	2	0	4	5	19° C.
9.00	4	3	0	2	6	
		Heated to 25° C.				
9.15	0	1	2	1	11	25° C.
9.30	2	2	1	1	9	
9.45	1	0	1	4	9	26° C.
10.00	2	1	1	0	11	
10.15	2	3	0	2	8	
10.30	2	0	2	1	10	
10.45	2	0	1	2	10	25° C.
		Cooled to 17° C.				
11.00	0	3	2	5	5	17° C.
11.15	6	0	0	5	4	14° C.
11.15	6	0	0	5	4	14° C.
11.30	5	3	1	2	4	
11.45	4	4	4	0	3	14.5° C.
12.00 M.	6	2	1	2	4	
Averages at low temperatures:	4.1	2.4	1.2	2.9	4.4	
Averages at high temperatures:	1.6	1.0	1.1	1.6	9.8	

The normal vertical position of daphnids exposed to horizontal light or to darkness will be determined, first by the geotaxis, which will vary with the light intensity and the temperature; and second, by the rate of locomotor activity, which will also vary with the light intensity and with the temperature. The relations of these factors is very complex, especially in view of the fact that the previous exposure to light and heat must be taken into account. Experiments 13 and 14 show that the tendency to go down on heating and up on cooling is persistent for a number of hours.

In general, high temperatures produce in *Daphnia pulex* a tendency to positive geotaxis, while low temperatures produce a tendency to negative geotaxis. These tendencies persist for at least a considerable length of time.

GEOTAXIS IN RELATION TO THE CHEMICAL CONTENT OF THE WATER

Oxygen: No definite change in vertical distribution could be observed on changing daphnids from water saturated with oxygen to water from which the oxygen had been driven off by boiling or by the reverse change.

Carbon dioxide: Carbon dioxide gas was bubbled for half an hour through a jar of tap water and this was then supposed to contain an extra amount of the chemical in solution. However, no change in the vertical distribution could be observed on changing daphnids into this water or back into normal tap water.

Food: No experiments were conducted on the effect of food as a factor affecting geotaxis, but it is probably not of importance in this respect.

Waste: One experiment was performed on the effect of waste materials on geotaxis. A very large number of daphnids were placed together in a tall sealed glass jar in the darkroom with weak horizontal light. The crowding was so great that all the adults had died before the end of 24 hours. During this time no change in geotaxis could be observed so it seems that organic waste products have little effect on geotaxis.

In so far as these observations and inferences are conclusive we find that changes in the chemical content of the medium have little effect on the geotaxis of the adults of *Daphnia pulex*.

GEOTAXIS IN RELATION TO MECHANICAL STIMULATION

It could not be determined that mechanical stimulation has any effect on the geotaxis of these daphnids. If such an effect is present it is either very weakly marked or is very temporary and can have little value in determining the vertical movements of the animals.

GEOTAXIS AT DIFFERENT TIMES OF THE DAY

A number of experiments were performed to determine if the geotaxis varies at different times during the day. The method used was to place a number of daphnids in a tall jar marked off into five divisions. The jar was completely filled with water and the top sealed by a glass stopper. In the darkroom the jar of animals was exposed to weak horizontal light. A count was made each hour of the number of individuals in each division of the jar, during a period of 30 hours. No periodicity in vertical distribution could be found, either in daphnids taken from daylight at the beginning of the experiment or in daphnids previously exposed to weak light for a day or more. We may then conclude that there is no diurnal rhythm of geotaxis in this species, except that dependent upon rhythmical change in the external physical factors.

LOCOMOTOR ACTIVITY IN RELATION TO LIGHT INTENSITY

Daphnids under natural conditions assume a position in the water with the head pointing upward. When no locomotor movements are being made the drag of the antennae on the water, as the weight of the body pulls the animal down, causes the daphnids to assume this posision. When strokes are made with the antennae the tendency then is to raise the animal vertically through the water.

The rate of sinking of adult daphnids 3 to 4 millimeters long with expanded antennae is stated by Birge (1897) to be at the rate of 20 to 30 centimeters per minute. Young daphnids 1 millimeter or less in length sink much more slowly at the rate of 5 to 10 centimeters per minute. This slower rate of sinking makes it much easier for the young daphnids to remain near the surface than it is for the adults.

It will be seen that it requires a certain rate of activity to maintain an individual at any certain height in the water. If the locomotor activity increases there will be a tendency for the animal to move to higher levels while a decrease of activity will allow it to sink.

Yerkes (1900) has shown that an increase of light intensity increases the speed of locomotion in *Daphnia pulex.* It can easily be observed that on a great increase of light intensity there is a decided increase of activity.

The increase of locomotor activity caused by increase of light intensity will have a tendency to cause the daphnids to move upwards, while a decrease of intensity slows down their activity and allows them to sink to lower levels.

LOCOMOTOR ACTIVITY IN RELATION TO TEMPERATURE

In studying the effect of temperature on locomotor activity a number of experiments were performed to determine the speed of motion toward a weak light at various temperatures. This method is not very satisfactory because the change in temperature causes changes in the phototaxis as well as in the locomotor activity and it is difficult to separate the effects of the two factors. Further, different individuals give very different and often contradictory results. The number of animals used in the averages is too small to give very great accuracy in conclusions. However, it is thought that some of the relations between temperature and rate of activity are indicated.

The method used was to mark off transverse lines 10 centimeters apart on the bottom of a glass dish. In the darkroom a 50 watt Edison lamp was placed 25 centimeters horizontally from each end of the dish. A daphnid was then introduced into the dish and allowed to swim toward one light. As soon as the animal passed the line marked off on that end of the dish this light was turned off and at the same time the light at the other end of the dish turned on. An observation consisted of 8 trips, 4 each way, of the animal across the dish. The time was recorded in minutes and seconds. In comparing the effects of change of temperature two dishes were used with the water kept at the different temperatures. Then the animals were gently shifted from one to the other by a large pipette.

In Experiment 16 each individual shows a decided increase of speed of travel toward a weak light on first raising the temperature 5 degrees. The averages for five individuals are 4′ 02″

at normal temperature and 2′ 46″ after heating. Also, the averages of all the observations show a higher rate of speed at the higher temperature. This effect is produced in spite of the fact that the phototaxis is lessened by the increase of temperature. In this case then we have a definite increase of locomotor activity by increase of temperature.

Exp. 16

Effect of heating on rate of locomotor activity

Time in minutes and seconds required to travel 80 cm. toward a weak light.

Temperature, C....	20.5°	25.5°	20.5°	25.5°	20.5°
Individual A	3′ 23″	2′ 50″	1′ 55″	2′ 23″	1′ 45″
B	2′ 20″	2′ 05″	1′ 05″	1′ 30″	1′ 45″
C	5′ 00″	3′ 00″	3′ 00″	2′ 25″	3′ 15″
D	4′ 55″	3′ 20″	4′ 40″	3′ 20″	4′ 55″
E	4′ 35″	2′ 35″	3′ 05″	1′ 55″	2′ 45″
Averages..........	4′ 02″	2′ 46″	2′54″	2′ 18″	2′ 39″

Average speed before change of temperature, 4′ 02″.
Average speed on first heating, 2′ 46″.
Average speed at 25.5° C., 2′ 32″.
Average speed at 20.5° C. after heating, 2′ 46″.

On cooling daphnids from a normal temperature of 20° C. down to 15° C. there is also an increase of speed of motion toward a weak light and the averages show very definitely a faster rate of speed at the low temperature than at the normal. However, the decrease of temperature increases the positive phototaxis and the increase in speed of travel may be due to this cause rather than to the lower temperature directly increasing the locomotor activity.

Experiment 17 shows the effect of continued exposure to a temperature of 25.5° C. This indicates that while the activity is increased when the temperature is first raised, after a short time the speed of travel decreases and soon the animal travels more slowly than at the normal temperature. It can be directly observed that a continued high temperature causes many of the daphnids to become very weakly positive and to show many erratic movements, even going at times directly away from the light. Many also grow very feeble and show a tendency to settle to the bottom of the dish. This is a real decrease of locomotor activity. However, other individuals show a continued high rate of locomotion after a lengthy exposure to the higher temperature.

Exp. 17

Activity on continued exposure to high temperature

Time in minutes and seconds required to travel 80 cm. toward a weak light.

Temperature, C.	20.5°	25.5°					
Exposure, minutes		0	15	30	45	60	90
Individual A	3′ 20″	3′ 08″	3′ 35″	2′ 10″	6′ 35″	5′ 20″	8′ 05″
B	3′ 05″	2′ 00″	2′ 17″	2′ 30″	3′ 15″	3′ 00″	2′ 10″
C	2′ 30″	2′ 10″	1′ 40″	1′ 30″	1′ 30″	1′ 35″	2′ 00″
D	3′ 30″	3′ 55″	4′ 40″	4′ 50″	6′ 30″	3′ 25″	5′ 00″
E	2′ 05″	2′ 20″	2′ 40″	3′ 15″	2′ 30″	3′ 00″	3′ 55″
Averages	2′ 54″	2′ 43″	2′ 58″	2′ 51″	4′ 04″	3′ 16″	4′ 14″

The effect of continued exposure to cold seems to be very irregular. Some individuals show a decrease of speed of travel on continued exposure to a temperature of 15° C., while others show an increase of activity under the same conditions. The results are too uncertain to base any definite conclusions upon.

Temperature, then, has a very irregular effect on locomotor activity. The most definite fact is that a sudden increase of 5 degrees above the normal causes an increase of activity, which persists for a short time.

LOCOMOTOR ACTIVITY IN RELATION TO THE CHEMICAL CONTENT OF THE WATER

The chemical content of the water is probably of importance in modifying the rate of locomotion of these animals, but no experiments bearing on this subject have been performed. As the chemical content of the water is subject to very little daily variation this factor cannot be a primary factor affecting diurnal migration although it might have some effect on the seasonal migrations.

LOCOMOTOR ACTIVITY IN RELATION TO MECHANICAL STIMULATION

Observations show that by strong mechanical stimulation, such as caused by shaking the dish, the locomotor activity is temporarily stopped. This allows the animals to sink downward. On the cessation of the stimulation the activity is, for a short time, greater than before.

LOCOMOTOR ACTIVITY AT DIFFERENT TIMES OF DAY

Experiments performed to determine whether a periodicity in vertical distribution occurred gave only negative results (see geotaxis in relation to time of day). The possibility may be considered that both geotaxis and activity have diurnal rhythms and that the activity decreases in the same degree that the negative geotaxis increases and the reverse. Such a condition is not believable. We may then feel confident that there is no diurnal rhythm in either, except such as is due to daily changes in the external physical factors.

THERMOTAXIS

Yerkes (1903) has shown that the radiant heat from a 16 candle-power incandescent lamp does not have an appreciable effect on the movements of *Daphnia pulex*. In darkness there is an irregular wandering away from a region heated to 29° C. This will evidently be of some importance in determining the vertical positions of the animals in lakes where the surface layers grow very warm in summer.

CHEMOTAXIS

No observations have been made as to the possibility of chemotaxis being a factor in the vertical movements of *Daphnia*. It can hardly be a very important factor, although it might have a modifying influence on behavior.

PRESSURE

The pressure acting at any given depth in a body of water will be very nearly constant at all times so that pressure changes cannot be a primary factor determining the movements of the plankton crustacea. As the animals move upward or downward in response to various other tendencies the changes in pressure experienced might be supposed to modify to some extent the action of these tendencies. However, the only experiment performed to test this supposition gave negative results. In this experiment an increase in water pressure roughly guessed at 15 pounds did not seem to cause any change in the vertical distribution of the animals. The extensive daily migrations performed by some species of *Daphnia*, 32 meters in *Daphnia hyalina* (Burckhardt, 1900), also argues against pressure being of importance in modifying the factors causing the vertical movements in this genus.

PART II. DISCUSSION

OBSERVED VERTICAL MOVEMENTS IN *DAPHNIA*

Below are given brief statements of some of the recorded observations of vertical movements in *Daphnia*, with especial reference to *Daphnia pulex.*

Juday (1904) found that in Oconomowoc Lake, Wis., in August the adults of *Daphnia pulex pulicaria* were at a depth of 10 meters in the daytime and reached the surface an hour after sunset. In doing so they moved up into water that was at least 15° C. warmer than that occupied by them during the day. At this time the young were found at a depth of 6 meters in the daytime, and reached the surface a half hour after sunset. Neither adults nor young were taken in a surface catch made an hour and a half before sunrise. In October, adults were found 13 meters below the surface in the daytime and were taken in a surface catch made two hours after sunset. In June, both adults and young were found at a depth of 1 meter in the daytime. The young reached the surface in the first half hour after sunset and the adults arrived there a half hour later. Both left the surface during the second half hour before sunrise.

In Okauchee Lake, Wis., in August, "young were found at a depth of 8 meters and adults at 9 meters in the daytime. Two and a quarter hours after sunset young were found at a depth of only 2 meters and adults 4 meters. In October, young were at a depth of 6 and adults 12 meters in the daytime. Three and a quarter hours after sunset the former were at the surface and the latter at 2 meters. In June, the day catches showed young at a depth of 1 meter and adults at 3 meters. The former appeared at the surface about half an hour before sunset and the latter about two hours after sunset. Both disappeared from the surface during the fifth half hour before sunrise."

Little indication of a diurnal movement by *Daphnia pulex pulicaria* was found by Juday (1902) in Winona Lake, Indiana.

In Lake Mendota, Wis., Birge (1895) found no diurnal movement in this species during the month of July. During that month the species was confined in the vertical space between depths of 6 and 15 meters, and very few were below 12 meters. In this lake the young of the species show a tendency to collect in the upper parts of the lake while the adults are found at lower levels (Birge, 1897).

Juday (1904) was also unable to find a diurnal movement of this species in Lake Mendota.

The seasonal movement of *Daphnia pulex pulicaria* is well marked in Lake Mendota. Table I, based on figures given by Birge (1897), shows that in winter the species is most abundant at the surface, but that as the water of the lake heats up the animals move downward until in August they are most abundant at depths of between 9 and 12 meters. In the fall they move upward until they again appear at the surface.

TABLE 1

Daphnia pulicaria

Percentage vertical distribution in Lake Mendota, Wis.
(From Birge, 1897, *Trans. Wis. Acad. Sci.*, Vol. 11.)

		Per cent. in each 3 meter level					
Depth, meters . . .		0–3	3–6	6–9	9–12	12–15	15–81
1895–1896							
July	16–31	0.0	0.0	53.1	12.5	32.8	1.6
August	1–15	0.0	0.0	11.0	65.0	22.0	1.0
August	16–31	0.0	1.6	2.3	80.2	14.8	1.0
September	1–15	0.0	2.2	4.5	68.8	22.6	1.8
September	16–30	0.0	1.5	2.2	3.4	58.8	33.7
October	1–15	14.1	13.8	14.1	19.2	17.1	21.7
October	16–31	22.5	21.9	22.3	12.7	9.6	11.0
November	1–15	42.7	27.3	8.7	9.2	5.5	6.6
November	16–30	25.2	29.2	19.6	15.1	5.7	5.2
December	1–15	51.6	35.5	7.9	2.8	1.9	0.2
December	16–31	37.8	31.1	11.4	11.1	7.7	0.9
January	1–15	68.3	14.5	12.7	3.5	0.5	0.5
January	16–31	77.9	8.4	8.4	2.1	2.1	1.1
February	1–14	75.8	9.1	5.0	2.8	2.4	4.8
February	15–29	43.4	20.3	8.7	11.5	8.7	7.3
March	1–15	....	....	....	....	....	....
March	16–31	34.0	18.9	27.0	9.4	7.6	3.2
April	1–15	10.4	14.6	31.2	25.0	12.5	6.3
April	16–30	84.9	10.6	0.8	1.5	1.7	0.5
May	1–15	13.1	16.2	19.5	12.0	16.7	22.4
May	16–31	28.0	16.9	18.8	14.5	10.0	11.7
June	1–15	17.5	10.0	15.0	21.3	10.1	25.8
June	16–30	1.9	6.2	11.7	16.0	45.8	18.5
July	1–15	0.0	0.9	8.6	27.0	57.0	6.5
July	16–31	0.0	0.0	62.8	33.4	2.0	1.8
August	1–15	0.0	10.0	17 0	71.0	2.0	0.0
August	16–31	0.0	0.0	0.0	80.0	20.0	0.0

On August 26, 1985, there was an alternation of cloud and sunshine over Lake Mendota and Birge (1897) observed that adult and young daphnids were approximately one meter below the surface during the sunny periods, but rose to one-half meter during the cloudy intervals. "The rise immediately followed the obscuring of the sun and the return was as prompt when the sun shone again."

The same author (1897) was unable to find that wind and waves affect the distribution of the plankton crustacea. The upper meter was fully occupied by them when the lake was almost too rough to venture out in a row boat. These results do not agree with those of Francé (1894), who found that in stormy weather the crustacea were found at a greater depth than during still weather.

In those lakes where the water in the lower levels becomes stagnant at certain periods in the year the crustacea are usually found to be entirely absent below the thermocline (Birge 1897). In these lakes the daphnids in their seasonal migrations move down, closely following the downward movement of the thermocline.

In the Vierwaldstättersee, Burckhardt (1900) observed a diurnal movement of *Daphnia hyalina* of about 32 meters during the early part of September. The mean depths of these daphnids at different times in the day on September 1st and 2nd are given below:

9 P.M. to 4 A.M. at 5 meters.
at 9 A.M. at 30 meters.
at 12 M. at 37 meters.
at 5 P.M. at 28 meters.

From the above observations, we find that there is often a diurnal migration in *Daphnia*, and that in such cases the animals are found nearest the surface at night and deeper in the lake during the day. This diurnal migration varies greatly in extent in different lakes and in different seasons. In Oconomowoc Lake, during October, there is a diurnal movement from a depth of 12 meters to the surface, while in the same lake in June the movement is only from a depth of 1 meter to the surface. In some lakes there is only a slight diurnal movement, while in others no diurnal movement has been found.

In many lakes there is an annual movement, which may be illustrated by the movement of *Daphnia pulex pulicaria* in Lake Mendota. Here the animals have a definite vertical range in the water at each season, this being near the surface in winter and deeper in the lake during the summer. Diurnal movement may occur at all seasons, but is confined within the limits of the range for the given season, so that at some seasons the diurnal movement does not reach the surface at any time during the day.

There is a marked difference between the movements of the adults and the young daphnids. The young animals are nearly always found nearer the surface than the adults, and move upward more promptly than the latter.

Storms cause the plankton crustacea to be found at lower depths according to some observers, but this does not seem to be always the case.

Cloudy weather causes the daphnids to be found nearer the surface than would be the case in clear weather.

Moonlight has been stated to result in driving the plankton crustacea to lower depths than the normal for a dark night.

These, then, are the movements of *Daphnia* whose causes are the object of study in this paper. While it will be impossible to discuss the factors governing the movements in each lake, because the physical factors have not been studied in sufficient detail, still, on the basis of the experiments described in the first part of this paper, it will be possible to suggest in many cases the probable relationship between the physical factors and the observed movements.

VERTICAL MOVEMENTS CAUSED BY CHANGES OF LIGHT INTENSITY

As sunlight passes down through the water of a lake it is gradually absorbed until at great depths there is absolute darkness. This result gives, in deep lakes, a range of light intensities from full sunlight to darkness. We have seen that *Daphnia pulex* is positively phototactic at intensities below the intensity of diffuse daylight. To intensities above this, at a temperature of 20° C., the animals are normally neutral. Only in high temperatures and strong light do they show a negative phototaxis. The positive phototaxis of the daphnids will prevent them from going much below the lower limit of neutral intensity, but, as far as the phototaxis is concerned, they might occur at any level in the neutral intensity. The range of light intensity to which the daphnids are neutral must extend over a considerable depth.

It has also been shown that the light intensity affects the geotaxis. The action of the positive geotaxis induced by strong or moderately strong light will probably be to cause the daphnids to go down until further motion downward is stopped by the beginning of positive phototaxis.

The most important change in light intensity acting on a lake is the change from sunlight to darkness occurring every day. If we suppose the daphnids to be at the surface at night, the first rays of light in the morning will cause a positive geotaxis which will overcome to some extent the positive phototaxis and the animals will begin to move downward. As the light increases in intensity they will continue to move downward, owing to the continued increasing positive geotaxis, and will keep near the lower limit of neutral phototaxis. The downward movement then is due to the action of light on the geotaxis, but the limit of downward motion is determined partly by the phototaxis. In the evening as the daylight fades the daphnids move upward, owing partly to the negative geotaxis caused by lowered light intensity, and partly due to the positive phototaxis caused by weak light. At night the daphnids remain near the surface due to the negative geotaxis existing in the absence of light. For the sake of simplicity in the above statement no account has been taken of the gradual changes in light intensity throughout the day.

It is evident that in the case of *Daphnia pulex* the change of geotaxis caused by changes in light intensity is the most important factor causing the diurnal migrations, while change of phototaxis is a factor merely limiting the extent of the movements. If there were no change in geotaxis there would be only a feeble indication of a diurnal migration in this species.

The reversal of phototaxis caused by the action of the ultra-violet rays might under some circumstances be a factor causing diurnal movement, but it seems that in this case the positive geotaxis caused by the action of the visible rays will keep these daphnids down below the action of the ultra-violet rays, so that the action of these rays will not be a factor in the vertical movements.

The light intensity effective on any given lake will vary at different seasons of the year. The lower limit of neutral light intensity for phototaxis should be at a much lower depth at midday in summer than at the same time of day in winter. For this reason the lower limit of daily movement in *Daphnia* should be deeper in summer than in winter. However, the range of motion may be less in summer than in winter owing to the effect of the higher temperatures of the surface waters in summer on the geotaxis. It seems that the change of the midday light intensities with the seasons will have a much smaller effect in determining the mean daily depth than will the changes in temperature.

Cloudy weather should have the effect of raising the mean vertical position of the daphnids. In partly clouded weather the passage of a cloud across the sun should reduce the light intensity enough to cause a tendency to negative geotaxis and positive phototaxis which would cause an upward movement of the animals. Clear sunshine following would produce a tendency to positive geotaxis and neutral phototaxis resulting in movement downward.

Very strong moonlight might cause a slight tendency to positive geotaxis and produce a small movement downwards.

Different lakes will be subjected to great differences in light intensity due to their position in latitude and altitude. The light will penetrate to very different depths in different lakes owing to the great variation in the clearness of the water. We should then not expect to find the same migration behavior in every lake.

VERTICAL MOVEMENTS CAUSED BY CHANGES IN TEMPERATURE

Few observations are at hand to show the variation during the day of the water temperatures at different levels in a lake, but this variation is much greater in shallow than in deep lakes. A table given by Hankinson (1907, p. 202) shows a variation of three degrees in the surface temperature, during May 29, in a shallow part of Walnut Lake, Michigan. The daily variations in temperature of some shallow lakes must be greater than this, but in most lakes the variation in the temperature of the surface water will be very small and there will be almost no diurnal variation in the temperature of the lower levels. Temperature changes, then, cannot have an important influence in causing the diurnal movements.

In summer the surface waters of an ordinary lake become warmed while, if the lake be deep enough, the lower levels remain cool (Table II).

TABLE II

Temperatures of Lake Cochituate, Mass.
(From Fitzgerald, 1893, *Trans. Amer. Soc. Civ. Eng.* 34(p. 96.)
(In degrees Centigrade calculated from the original Fahrenheit.)

Depth in feet		0	5	10	15	20	25	30	40	50	60
April	18	5.5°C.	5.5°C.	5.5°C.	5.5°C.	5.5°C.	5.5°C.	5.5°C.	5.6°C.	5.6°C.	5.7°C.
May	16	15.2	14.7	11.9	9.3	9.0	8.9	8.5	8.3	8.3	7.5
June	20	22.7	22.5	21.9	17.9	17.5	14.4	9.3	8.6	8.3	7.4
July	18	24.6	23.9	23.8	18.0	11.4	10.1	9.1	8.6	7.9	7.2
August	15	23.7	23.4	21.9	20.6	13.3	11.8	9.4	8.4	7.7	7.2
September	19	18.4	18.4	18.4	18.1	14.6	12.1	10.7	9.2	9.2	7.1
October	17	13.6	13.6	13.6	13.6	13.5	12.4	11.5	8.8	7.9	7.2
November	21	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.3
Averages....		16.9	16.6	16.0	14.2	11.5	10.3	9.3	8.3	7.9	7.2

It is evident that in performing any considerable migration near the surface in summer the daphnids will be subjected to a considerable variation of temperature. If we consider them moving downward in the early morning in response to increase of light intensity they will be moving into water at lower and lower temperatures. These low temperatures will have a tendency to produce negative geotaxis and positive phototaxis. These tendencies will operate to reduce the range of the downward movement. On moving upward in the evening the animals will be reaching increasing temperatures of water. These higher temperatures will have a tendency to produce positive geotaxis. If the surface temperature is in the neighborhood of 25° C. there will be a slowing up of the locomotor activity after a short exposure to that amount of heat. Irregular wandering away from the high temperature may also be operative. These factors will then work together to lessen the distance of upward travel in summer. Then, in a lake where the surface water is much warmer than the under layers we would expect that the range of diurnal migration would be much reduced.

In winter, when all the water of the lake is at nearly the same temperature we would expect rather large migrations

However, the sunlight is much reduced at that season, causing a tendency toward positive phototaxis. Also, the low temperature of the water causes a tendency toward negative geotaxis and positive phototaxis. All of these factors tend to keep the animals near the surface at all times and so cut down the range of migration at that time of year.

In different lakes the conditions of temperature will be very varied and this will have a great effect in causing the observed variations in the range and the peculiarities of the diurnal migration found in different lakes. The differences in the temperatures are particularly great between shallow and deep lakes.

As stated above, the low water temperatures of winter will have a tendency to keep the daphnids near the surface. In summer the increase in temperature of the surface layers will cause the animals to occupy lower levels. Diurnal movements may take place in summer as well as in winter, but in summer the limit of movements will be at lower levels than in winter.

Changes in temperature, then, are not the primary cause of diurnal movement, but difference in temperature of the water at different levels in a lake may operate to shorten the distance of the diurnal movement. Changes in water temperature, particularly of the surface layers, at different seasons of the year is the principal factor determining the seasonal movements. This result is chiefly due to the effect of different degrees of temperature on geotaxis, although the effect of temperature on phototaxis has a minor effect.

MOVEMENTS CAUSED BY MECHANICAL STIMULATION

The mechanical stimulation most likely to affect the plankton crustacea will be the action of the waves. It has been stated in a previous section that mechanical stimulation, while it continues, tends to inhibit the locomotor activity of the animals so that they fall passively through the water. After descending to a depth where the wave action could no longer be felt the daphnids would tend to rise again until stopped by reaching a region of perceptible wave action. The result is that the daphnids should be found at a lower level than normal on stormy days, and by this reaction escape the damaging action of strong waves.

VERTICAL MOVEMENTS CAUSED BY CHANGES IN THE CHEMICAL CONTENT OF THE MEDIUM

The chemical content of the water of an ordinary lake will be subject to changes in the proportion of dissolved food substances, in oxygen content, in the amount of dissolved carbon dioxide, and in the proportion of organic waste products.

Changes in the proportion of carbon dioxide is the only factor likely to be of importance in the vertical movements of *Daphnia.* This substance has a tendency to produce positive phototaxis. In the stagnant water found at certain seasons below the thermocline in some moderately deep lakes, the excess of carbon dioxide will perhaps increase the positive phototaxis of the daphnids enough to cause them to rise to a better ventilated stratum. Otherwise changes of the chemical content of the medium do not seem to be of great importance in determining the vertical movements of *Daphnia.*

VERTICAL MOVEMENTS CAUSED BY AGING OF INDIVIDUALS

Although no careful study has been made of the reactions of any age of the daphnids except the adults, it can easily be observed that the young daphnids show marked differences in behavior from the behavior of the adults. In general the young are more strongly positively phototactic and more strongly negatively geotactic than the adults. They sink less rapidly through the water than the adults. All these features tend to cause the young daphnids to be found on the average nearer the surface than the adults. In many cases the adults reach the surface at some time in the day and in winter they may remain near the surface all day, but in general the adults are found at deeper levels than the young. In the life of the individual there must then be a movement of the average daily position downward through the water until death occurs and the dead body sinks to the bottom. In lakes where the lower levels are stagnant the daphnids will likely be killed soon after they drop below the thermocline.

Reproduction seems to occur in periods. Birge (1897), in Lake Mendota, found one period in the fall and several in the spring. During a period of reproduction young daphnids appear in great numbers and crowd toward the surface. Being in much greater numbers than the adults the percentages of distribution indicates an upward movement of the species. As the individuals grow older they tend to drop into lower levels, and through natural mortality grow few in number.

We must, then, distinguish a periodicity in vertical distribution due to the aging of individuals and the occurrence of reproductive periods.

GENERAL FEATURES OF BEHAVIOR IN *DAPHNIA*

After a considerable study of these daphnids the conclusion is forced on one that they do not behave in a perfectly mechanical manner. They are not little machines which will respond in a definite way each time a definite change is made in the environment. A glance at almost any of the tables included in this paper will make it clear that although there is a tendency to a definite kind of behavior when any particular one of the environmental factors is altered, yet a small proportion of the animals will not react in that particular way, but may even react in a manner directly contrary to the behavior of the majority. It may be that with more exact and thoroughgoing methods of research many of the apparent exceptions could be shown to be due to normal processes. At present the best we can do is to say that environmental changes tend to produce changes in the condition of the animal and that it then reacts differently than before.

In this paper it has been the aim to show the normal tendencies in behavior when a single factor is varied and the others kept constant or eliminated as not contributing to the results. When possible a number of animals were used in the same experiment so that quantitative results were secured. Where this was not possible the results have been checked by a number of repetitions of the experiment or by other methods of control.

In cases where several environmental factors vary at the same time the behavior becomes quite complex and it is difficult to determine in such cases which factor is the more potent and what the resultant behavior will be.

In the previous part of this paper much use has been made of such terms as phototaxis, geotaxis, etc. It is not intended by the use of such expressions to subscribe to any particular theory as to the basis of animal behavior. By the use of these terms it is intended only to express the tendency to move toward or from a source of stimulation. Whether this is due to a tropism caused by unequal stimulation on the two sides of a bilaterally symmetrical organism, or whether the orientation to the stimulus results from the action of trial and error need not concern us here.

It seems that most of the behavior of *Daphnia* is determined by orientation of the body to different sources of stimulation. However, the random movements which occur on exposure to strong light, great cold, or great heat give a means of escape from unfavorable conditions, but secure this result without a definite orientation of the body.

It may be observed that while many of the previously given experiments show tendencies to upward movement it is very seldom that all the animals go to the upper part of the dish. In the experiments showing a tendency to go toward the bottom this tendency is likely to be very strongly marked. It might be argued, then, that the upward movement is not due to a negative geotaxis, but is merely an irregular wandering which naturally would carry many of the animals toward the surface when the factors holding them down were no longer operative. However, it may be observed in many cases, particularly on shading a tall jar of daphnids exposed in sunlight, that there is an immediate and vigorous upward movement. The failure of some to move to the top when the tendency is in that direction must be due in part to the weight of the body, which has a constant tendency to drag the animal down. It is probably also due in part to the unnatural conditions under which the animals were kept. It was observed that daphnids freshly collected from natural ponds showed a greater tendency to upward movement than those kept for a long time in the laboratory. There is the further fact that the jars used for experimentation have a very slight depth in comparison with the average depth of a lake so that the available range of movement was very small. In nature the daphnids do not go to the very surface of the water or they would be caught on the surface film.

The reactions of the animals in moving upward or downward in response to changes in light intensity or temperature might be considered to be due to a change in the reaction of the organism to pressure rather than to gravity. It can be observed that daphnids under constant conditions maintain themselves at nearly a definite height in the aquarium. They may sink several centimeters, but usually soon regain the former position by a few rapid strokes of the antennae. Birge (1897) seems to be of the opinion that change of pressure is the controlling factor in this case. It seems that the differences in water pressure on the upper and lower parts of a daphnid must be very small in amount, and that these differences can hardly act as a directive force in the vertical movements. However, careful experimentation is needed to settle this point.

Although every care was taken to experiment on the animals under as nearly natural conditions as possible, it was not possible to reproduce the conditions of the natural habitat and still be able to control the factors for experimentation. The unnatural conditions in the experiments may have altered the behavior to some extent, but it is believed that the general features of daphnid behavior are as have been indicated.

Daphnia pulex shows a strong tendency to avoid any solid objects, such as the sides of the dish. This indicates that is is a true plankton animal.

When a daphnid is approached by a glass rod or other solid object held in the hand there usually ensues a vigorous movement away from the source of stimulation. This reaction must be of great value to the animals in escaping enemies.

When any considerable change is made in the environment, such as changing the animals to water to which they are not accustomed, or by strong heating or cooling, there is a tendency for a great number to get caught on the surface film. Once caught on this film the animals are seldom able to escape but remain there until they are exhausted and die.

The behavior of *Daphnia pulex* is regulatory in general. Continued exposure to temperatures much above 25° C. produces feebleness or death in these animals. However, in nature such strong stimulation would produce positive geotaxis and perhaps negative phototaxis which would cause the animals to descend to lower levels in the lake wehre the temperature would be lower. Under ordinary conditions the animals remain near the surface where they find food and the normal conditions of existence.

One particular case of very peculiar behavior may be mentioned. A number of individuals of *Daphnia pulex* collected from a small pond on the morning of February 5th showed very strong positive phototaxis in sunlight. As a further abnormality these individuals showed the peculiarity of changing temporarily from positive to negative phototaxis when the light intensity was reduced by shading the dish.

Very likely other factors besides those considered will be found to be operative in affecting the vertical movements of *Daphnia*, but it seems likely that the more important factors have been mentioned.

REVERSAL OF GEOTAXIS IN OTHER PLANKTON ANIMALS

Reversal of geotaxis by changes in light and temperature similar to that found in *Daphnia pulex* has been observed by previous authors in several different groups of plankton animals. A brief reference will be made to some of these observations.

Esterly (1907) found that the females of *Cyclops albidus* were positively geotactic in daylight, but were negatively geotactic in darkness.

It was observed by McGinnis (1911) that *Branchippus serratus* is positively geotactic in light and negatively geotactic in darkness.

An increase of light makes *Balanus* larvae positively geotactic, while a decrease of light makes them negatively geotactic (Ewald, 1912). After a certain exposure to light of any intensity they assume a general distribution in respect to gravity.

The phantom larvae of *Corethra* become positively geotactic in sunlight or strong electric light (Harper, 1907).

Macropsis, a plankton schizopod of the family Mysididae, is always positively phototacitc, but in light from above the animals remain at the bottom of the vessel (Bauer, 1908). Perhaps it will be possible to show that this behavior is due to light causing a positive geotaxis which is more potent than the positive phototaxis.

Loeb (1893) states that *Polygordius* larvae may be made negatively phototactic by heating or by intense light, and that the geotaxis is always positive when the phototaxis is negative and negative when the phototaxis is positive. No such correlation as this is found in *Daphnia pulex*.

Massart (1891) found that the geotaxis of *Chromulina woroniniana*, a spirillum, is positive at temperatures of from 5° to

7° C., while it is negative at from 15° to 20° C. These organisms are found on the surface in summer, but in winter they gather at the bottom of the body of water in which they occur. The relation of temperature to geotaxis in this case is the reverse of the relation found to occur in the other cases mentioned above.

These observations on plankton organisms of several distinct orders and classes go to show that reversal of geotaxis through the agency of changes in light and temperature is a rather widespread phenomenon. The importance of such a reversal of geotaxis in determining the vertical movements of plankton animals must be very great.

SUMMARY

In the experimental part of this paper it has been shown that the individuals of *Daphnia pulex* are normally positive to weak light at a temperature of 20° C. At that temperature they are normally indifferent to light intensities stronger than weak diffuse daylight.

Increase of temperature has a tendency to decrease the positive phototaxis, while decrease of temperature tends to make the animals more strongly positive. At temperatures below 12° C. they are positive to all light intensities.

Increase of light intensity causes a tendency to positive geotaxis, while decrease of intensity causes a tendency to negative geotaxis. These tendencies seem to persist for at least a considerable period of time.

High temperatures produce a tendency to positive geotaxis, while low temperatures cause a tendency to negative geotaxis. These tendencies seem to be very persistent.

The diurnal movements of *Daphnia pulex* are caused chiefly by variations in geotaxis induced by changes in light intensity. The limits of the diurnal movement are determined by the factors effective in producing the seasonal movements.

Change in geotaxis caused by changes in the temperature of the lake at different seasons of the year is the principal factor determining the seasonal movements of this species. The effects of the changes in temperature on phototaxis, and of the seasonal changes in the midday light intensities on geotaxis and on phototaxis are minor factors in this movement.

Strong wave action may cause a temporary inhibition of locomotor activity and this allows the animals to sink to lower levels.

No definite vertical movement due to changes in the chemical content of the water, or to the action of a diurnal rhythm, independent of the effect of recurrent external physical changes, could be found.

Young individuals are more strongly positively phototactic and negatively geotactic than adults. They also sink less rapidly in water. For these reasons they are usually found nearer the surface than the adults. There is a downward movement due to the aging of the individuals.

Much of the behavior of *Daphnia* is determined by orientation to various stimuli, but some regulatory behavior is obtained by means of random movements.

Change in geotaxis by changes in light intensity and in temperature has been observed in other plankton organisms, and is probably of widespread importance in determining the vertical movements of the plankton.

LITERATURE

BAUER, VICTOR. Über die reflektorische Regulierung der Schwimmbewegungen 1908. bei den Mysiden mit besonderer Berücksichtitung der doppelsinnigen Reizbarkeit der Augen. *Zeitschr. f. allgem. Physiol.*, **8**: 343-369.

BIRGE, E. A. Plankton Studies on Lake Mendota. I. The Vertical Distribution 1895. of the Pelagic Crustacea during July, 1894. *Trans. Wis. Acad.*, **10**: 421-484.

1897. Plankton Studies on Lake Mendota. II. The Crustacea of the Plankton from July, 1894 to December, 1896. *Trans. Wis. Acad.*, **11**: 274-448.

1897a. The Vertical Distribution of the Limnetic Crustacea of Lake Mendota. *Biol. Cent.*, **17**: 371-374.

BURCKHARDT, G. Quantitative Studien über das Zooplankton des Vierwald- 1900. stättersees. *Mitteilungen der Naturforschender Gesellschaft Luzern*, 3 Heft, 1-309.

DAVENPORT, C. B., and CANNON, W. B. On the Determination of the Direction 1897. and Rate of Movement of Organisms by Light. *Jour. Physiol.*, **21**: 22-32.

DAVENPORT, C. B., and LEWIS, F. T. The Phototaxis of *Daphnia*. *Sci. N. S.*, 1899. **9**: 368.

ESTERLY, C. O. The Reactions of *Cyclops* to Light and to Gravity. *Amer. Jour.* 1907. *Physiol.*, **18**: 47-57.

EWALD, W. F. Über Orientierung, Lokomotion, und Lichtreaktionem einiger 1910. Cladoceran. *Biol. Cent.*, **30**: 1-16, 49-63, 379-384, 385-399; 4 figs.; 8 curves.

1912. On Artificial Modification of Light Reactions and the Influence of Electrolytes on Phototaxis. *Jour. Exp. Zool.*, **13**: 591-612.

FITZGERALD, DESMOND. The Temperatures of Lakes. *Trans. Amer. Soc. Civ.* 1895. *Eng.*, **34**: 67-109; 12 tables; 11 curves.

France, R. H. Zur Biologie des Planktons. *Biol. Cent.*, **14**: 33-38.
1894.

Frisch, Karl V., und Kupelwieser, Hans. Über den Einfluss der Lichtfarbe
1913. auf die phototaktschen Reaktionen niederer Krebse. *Biol. Cent.*, **33**: 518-552; 9 figs.; Taf. 3-5.

Groom, T. T., und Loeb, J. Der Heliotropismus der Nauplien von *Balanus per-*
1890. *foratus* und der periodischen Tieferwanderunden pelagischer Tiere. *Biol. Cent.*, **10**: 160-177.

Hankinson, T. L. A Biological Survey of Walnut Lake, Mich. *Rept. Mich.*
1908. *Geol. Sur.* for 1907, 157-288; pl. 13-75.

Harper, E. H. The Behavior of the Phantom Larvae of *Corethra plumicornis*
1907. Fabricus. *Jour. Comp. Psychol.*, **17**: 435-456.

Jensen, Paul. Ueber den Geotropismus niederer Organismen. *Archiv. f. d.*
1893. *ges. Physiol.*, **53**: 428-480; 17 figs.

Juday, Chancey. The Plankton of Winona Lake. *Proc. Ind. Acad.* for 1902,
1902. 120-133.
1904. The Diurnal Movement of Plankton Crustacea. *Trans. Wis. Acad.*, **14**: 534-568.

Loeb, J. Der Heliotropismus der Thiere und seine Uebereinstimmung mit dem
1889. Heliotropismus der Pflanzen. Würzburg. 118 pp. Trans. in Studies in General Physiology, 1905 (see below).
1893. Über künsliche Umwandlung positiv heliotropischer Thiere in negativ heliotropische und umgekehrt. *Arch. f. d. ges. Physiol.*, **54**: 81-107. Trans. in Studies in General Physiology, 1905 (see below).
1893a. On the Influence of Light on the Periodical Depth-Migrations of Pelagic Animals. *Bull. U. S. Fish Com.*, **13**: 65-68.
1905. Studies in General Physiology. Chicago. Vol. I, 423 pp.
1906. Ueber die Erregung von positivem Heliotropismus durch Saüre, insbesondere Kohlensaüre, und von negativem Heliotropismus durch ultraviolette Strahlen. *Arch. f. d. ges. Physiol.*, **115**: 564-581.

McGinnis, Mary O. Reactions of *Branchipus serratus* to Light, Heat, and Grav-
1911. ity. *Jour. Exp. Zool.*, **10**: 227-240.

Massart, Jean. Recherches sur les organismes inferieurs. III. La sensibilité a la
1891. Gravitation. *Bull. Belg. Acad.*, ser. 3, t. 22, 158-167.

Mast, S. O. Light and the Behavior of Organisms. New York. xi—410 pp.
1911.

Moore, A. R. Concerning Negative Phototropism in *Daphnia pulex*. *Jour. Exp.*
1912. *Zool.*, **13**: 573-575.

Ostwald, W. Zur Theorie der Richtungsbewegungen niederer schwimmender
1907. Organismen. III. Über die Abhängigkeit gewisser heliotropischer Reaktionen von der inneren Reibung des Mediums, sowie u. d. Wirkung "mechanischer" Sensibilatoren. *Arch. f. d. ges. Physiol.*, **117**: 384-408.

Parker, G. H. The Reactions of Copepods to various Stimuli and the bearing
1901. of this on daily Depth Migrations. *Bull. U. S. Fish Com.*, **21**: 103-123.

Yerkes, R. M. Reaction of Entomostraca to Stimulation by Light. II. Reac-
1900. tions of *Daphnia* and *Cypris*. *Amer. Jour. Physiol.*, **4**: 405-422.
1903. Reactions of *Daphnia pulex* to Light and Heat. Mark Aniv. Volume, 359-368.

STUDIES ON THE PHYSIOLOGY OF REPRODUCTION IN THE DOMESTIC FOWL. VII. DATA REGARDING THE BROODING INSTINCT IN ITS RELATION TO EGG PRODUCTION [1]

RAYMOND PEARL

INTRODUCTION

The extensive poultry plant maintained by the Maine Agricultural Experiment Station for experimental purposes offers an exceptional opportunity for the study of the habits, instincts, and behavior in general of the domestic fowl. While hens have been kept under domestication for a very long time, comparatively little systematic study of their adult behavior has ever been made. A splendid field of work is open here for the student of animal behavior. The writer and his associates are collecting data in certain directions within this field. Particular attention is being paid to those features of behavior which have to do with the processes of reproduction. It is the purpose of this paper to present a part of the material which has been collected regarding the brooding instinct in the hen. This material in part illustrates some facts which have not, so far as the writer is aware, hitherto been brought specifically to the attention of workers in animal behavior, and in part, it is believed, brings to light some new facts. This paper is in no way to be regarded as an exhaustive treatise of the subject of broodiness. Certain of the problems involved demand an extensive and detailed statistical treatment and our data on these are left for discussion at another time.

The brooding instinct belongs in the category of what Herrick (3) has well called " cyclical instincts." This author has pointed out that primitively the following cycle of events appears in the reproductive activity of birds: " (1) Spring migration; (2) courtship and mating (often attended by song); (3) selection of nesting site and building nest (often accompanied by fighting instinct); (4) egg-laying; (5) incubation—including care of eggs such as shielding, rolling, cleaning and covering (fear often completely blocked by brooding instinct); (6) care of young in nest ————; (7) care and incidental education of young when out of nest; guarding, feeding, play and other instinctive acts; (8) fall migration." In the domestic fowl, in spite of its long domestication and sophistication in regard to such unnatural things as trapnests and the like, all the instinctive acts enumerated in this list, with the exception of its first and last alone, occur with greater or less degrees of complexity and precision. Even such matters as sexual selection (preferential or assortive mating) and nest building, which domestication might be supposed to have done away with long since, may be observed in the poultry house and yard under proper conditions. We are, however, at present concerned only with five in the series, that is, the instinct for incubating the eggs, or of brooding.

---

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 65.

Herrick (*loc. cit.*) further says: "Beginning at 2, 3, or 4, according to circumstances, the cycle may be repeated once or oftener within the season." In another paper the same author (4) discusses a number of interesting cases of repetition and blending of the different members in this series of cyclical instincts. In certain of the domestic races of poultry, the repetition of the part of the cycle involving at least items 3, 4 and 5 within one season is of such frequent occurrence as to be regarded as a more or less normal condition. Whether or not the same is true of the wild species of *Gallus* it is impossible to say with certainty. Apparently no systematic study of the mating and breeding behavior of the wild *Gallus* has ever been made. The information to be gained from casual notes of travelers or hunters is meager and indefinite. Tegetmeier (9) in a discussion of the habits of the jungle fowl quotes from a "well-known Indian ornithologist who has published the results of his observations in *The Field* under the signature of Ornithognomon" to the following effect (*loc. cit.* pp. 259–260): "The period for incubation varies according to locality, but is generally at the beginning of the rains—i.e., June. I have seen eggs, however, in March, and Jerdon says the hen breeds as early as in January and as late as July. She selects for this purpose some secret thicket in the most retired and dense part of the jungle, scraping together a few leaves on the ground by way of nest. She remains as part of the cock's seraglio until some seven or ten or a dozen eggs have been deposited in the above spot, to which she stealthily repairs every day, and finally quits her party and retires alone and unseen to perform the duties of incubation."

In the case of the domestic fowl it has long been known that the brooding instinct could be aborted by proper treatment. This is obviously an important matter when hens are kept for egg production. Since a hen lays no eggs while broody the sooner the desire to " sit " can be overcome the sooner will she be brought back to the profitable performance of her duty as an egg producer. The usual method adopted for overcoming the tendency to brood is to confine the bird in a small coop with a slatted or bare board floor. Usually in a comparatively short time the tendency towards broodiness will disappear and if the bird is then put back under normal conditions she will again commence to lay, and may continue to do so for some time before the onset of another spell of broodiness. Just why this treatment should be so effective as it actually is, is not entirely clear. Formerly it was supposed to be necessary to " cool the blood " in order to " break up a sitter," and the somewhat drastic treatment of dipping the bird in a bucket of ice water was practised. It is probable that the chief factors concerned in producing the good results following confinement in a small coop are (1) that the bare floor and absence of eggs gives no encouragement to the bird to " sit," but on the contrary acts as a set of stimuli strongly antagonistic to this phase of instinctive behavior and (2) that the sudden change of conditions acts to upset the more or less delicately balanced physiological and psychical condition which characterizes the broody bird.

The instinct of brooding varies greatly in different breeds of domestic poultry. Some breeds—notably those classed by poultrymen as Mediterranean—have the instinct very slightly developed. Others—for example certain of the Asiatic breeds—go to the other extreme and have the instinct very strongly developed. The so-called American breeds, on the whole, occupy an intermediate position in this regard. With them the usual or normal course of events relative to broodiness is as follows.

1. During the winter months a number of eggs are laid. This constitutes what may be considered a first clutch.
2. Sometime in the early spring the hen stops laying and becomes broody. If she is not allowed to incubate eggs the broodiness disappears after a varying length of time depending on circumstances.
3. She lays another clutch of eggs, and
4. Becomes broody again, and so on.

This sequence of events—a period of laying followed by a period of brooding—may be repeated several times over. Usually after early summer the tendency to broodiness becomes greatly diminished or disappears altogether.

It will be seen that this series of events is very similar to a repeated cyclical instinct in wild birds. The normal sequence is broken into at the brooding stage by the fact that the hen is not allowed to incubate. She then begins anew at the next preceding phase of the cycle, viz., egg-laying. Now while this sequence of events is undoubtedly to be regarded as the normal one for so-called "broody" breeds of domestic poultry, there are numberless variations from it in individual cases. In this paper some of these variations will be described and discussed.

It should be noted that the behavior ordinarily classed by the poultryman inclusively as "broodiness" really belongs in two rather distinct categories. In the first place there is (a) the instinct to sit upon and incubate eggs. This is in many respects an altogether different thing than (b) the instinct to "brood" a flock of little chicks after they are hatched. The two forms of behavior are of course closely related to one another, and objectively have a number of features in common. But there are also marked differences. It is important to emphasize at this point that the present paper has to do entirely with the first of these instincts, namely that of incubation. In accordance with general usage, I have employed the terms "broodiness," "broody," etc., to designate this instinct. I desire, however, to make perfectly clear the restricted sense in which the terms are here used.

THE NATURE AND METHOD OF COLLECTION OF THE DATA

In the poultry work of this Station the only sort of nests provided for the laying birds are trap nests. Consequently, with the exception of an occasional egg laid on the floor (*Cf.* Pearl [5]), a record is obtained of every egg laid and of the hen which laid it. It is further the practice to confine birds which are broody in small coops until the particular manifestation of the instinct shall have disappeared. Beginning in December, 1907, and continuing until the present time, the practice has been followed of making a record of the date on which any bird is put into confinement for broodiness, and also of the date on which she is released from confinement as "cured." These records were made by putting "B" in the space corresponding to the date of onset of broodiness and "O" in the space corresponding to the date of release, on the poultry house egg record sheets. Records so obtained form the material of this paper. The records here discussed came, in the main, from 850 Barred Plymouth Rock pullets hatched in the spring of 1907. This breed will alone be considered in this paper.

In a critical consideration of these data the question at once arises as to their accuracy. Does the instinct of brooding manifest itself with such clearness that the recorded date of onset corresponds substantially with the actual? And further, to what extent does the date of release measure the actual subsidence of the instinct? These questions may be considered in order. The onset of a period of broodiness is, *at a certain stage*, marked by a characteristic behavior which is immediately and certainly recognizable by an experienced poultryman. Whether the stage at which this characteristic behavior begins marks the absolute beginning of the physiological state which underlies the instinct of broodiness is a question impossible of answer and really of no particular significance from the present standpoint. This behavior is the objective criterion of broodiness. Whatever preliminary internal or subjective stages the bird may go through leading up to this objective behavior constitutes a field of inquiry separate from the study of the behavior itself. This leads to the question as to whether the behavior connected with the onset of broodiness is so characteristic as to be easily and certainly recognizable. Of this there can be no doubt. The following characteristics are perfectly definite and obvious.

1. Continued sitting on the nest. As soon as she is thrown off the nest, the "broody," in the early stages, promptly returns.

2. A peculiar "clucking" note, not made by the bird at any other time in her life.

3. A raising of the feathers over the whole body, giving the bird a ruffled and very much enlarged appearance.

4. A marked pugnacity of behavior when anything approaches the sitting bird.

This brief statement gives an idea of the criteria of broodiness used in actual practice by the poultryman. When a bird exhibited these symptoms in a characteristic manner, she was confined and a " B " entered on the record. The records of *onset* of broodiness discussed in this paper can be unreservedly accepted as accurate and complete.

Turning to the " O " or release records, the case is somewhat different. A bird is in practice released from the detention coop when she no longer exhibits the symptoms of broodiness but instead appears normal in her behavior. Now since, as a matter of fact, there is not a sudden disappearance of the manifestation of broodiness following confinement, but instead a gradual subsidence of the symptoms, it must be clear that the time when a bird shall be released is an extremely difficult matter to decide. And further, records of the dates of release do not possess anything like so precise a metric significance as do dates of incarceration, so far as the manifestations of the instinct of brooding are concerned. The observer will frequently make the mistake of releasing a bird too soon and there will be an immediate recrudescence of the broodiness under the conditions of freedom, necessitating a second confinement. Or again, there is reason to suppose that sometimes the birds are kept in confinement too long. Evidence of this is given in cases where the bird lays on the same day that she is released. All that can be said regarding the release records is that every care was taken to make them as accurate and significant (i.e., in relation to the cessation of the manifestation of broodiness) as possible. From the nature of the case, however, they are not and cannot be *precise* records. This means that a great deal of caution must be exercised in drawing conclusions from them, and each individual case must be considered critically.

With these statements as to the character of the data in hand, attention may be turned to some actual records selected to bring out the following points:

1. Broodiness as a cyclical instinct.

2. Recurrence of brooding instinct with different degrees of intensity in the same hen.

3. Occurrence of brooding instinct outside of the breeding or mating season.

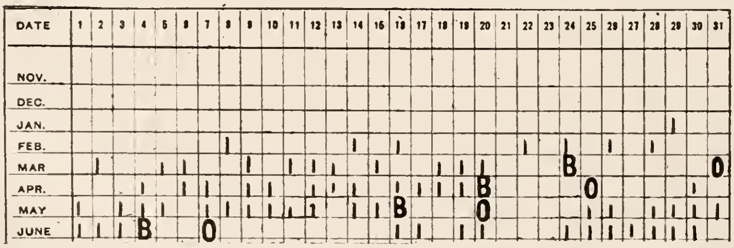
4. Broodiness not preceded by egg laying, or by very little egg laying.

5. The brooding instinct manifested with a very slight degree of intensity.

It should be said that all records of broodiness are exhibited in the form of tables giving the daily egg records of the birds. A single vertical stroke in the space corresponding to any given date signifies that on that date the bird which is the subject of the record laid an egg, while a blank space denotes the confinement of the bird on that date because she showed the characteristic symptoms of broodiness. An " O " signifies that the bird was released from confinement " cured " on the date indicated.

BROODINESS AS A CYCLICAL INSTINCT

It has been pointed out above that the normal course of events respecting broodiness in domesticated poultry is to be regarded as a sequence of egg-laying periods and periods of brooding. Table 1 embodies a record showing in a very clear and somewhat extreme form the instinct of brooding occurring in this cyclical fashion.



DATE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
NOV.																															
DEC.																															
JAN.																													I		
FEB.								I						I		I						I		I		I		I			
MAR		I			I	I			I		I	I	I		I			I	I	I				B							O
APR.				I		I	I		I	I		I	I	I		I	I	I	I	B					O					I	
MAY	I		I	I	I		I	I	I	I	I	I		I	I	B				O					I	I		I	I	I	I
JUNE	I	I	I	B			O									I	I		I	I				I	I	I	I	I	I	I	

FIGURE 1. Egg record of bird No. 139.

From this figure it is seen that in bird No. 139 the first appearance of broodiness was on March 24, following the laying of 19 eggs. On the eleventh day following—seven of these days having been spent in the detention coop—she began laying again. After laying 12 eggs she became broody again on April

20. On the tenth day following laying was again resumed and 13 eggs were laid before broodiness again appeared on May 16. On the ninth day following laying was resumed and 9 eggs were laid before the appearance of the last recorded period of broodiness beginning June 4. In this record the regular periodicity in the recurrence of the brooding instinct, particularly as measured by the number of eggs laid in the intervening "clutches," is striking. It will further be noted that in no case is the duration of the "broody" period, as measured by the number of days intervening between the laying of the last egg in one "clutch" and the first egg in the next, even approximately as great as the normal period of incubation of the hen's egg, 21 days. The treatment by confinement aborts the brooding instinct. Another point worthy of note is that the date of release, which indicates the disappearance of visible symptoms of broodiness, in each case precedes the date of beginning of the next "clutch" by some days.

DATE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
NOV.																															
DEC.																															
JAN.																															
FEB.				I		I	I				I		I		I	I	I		I	I	I	I	I		I	I	I	I	I		
MAR	I		I	I	I		I								I			I	I		I	I	I	I	I	I	I		I	I	I
APR.	I	I	I	I	I	I		I	B					0I	I		I	I	I	I	I	I	I	I	I	I	I	B			
MAY					0	I	I		I	I	I	I	I	I	I	I	B						0	I			I	I	I	I	
JUNE	I	I	I	I	I	B					0					I	I	I	I	I	I	I	I	B		0					

FIGURE 2. Egg record of bird No. 75.

Another record of the same general type as the last, but involving some different features is shown in Fig. 2.

This record shows the occurrence of 5 periods of broodiness with intervening "clutches" of 13, 10, 10 and 8 eggs. The first period of broodiness occurred in the height of the breeding season (April 9) and the instinct was evidently asserting itself at this time with slight intensity. This is indicated by the fact that only 4 days intervened between incarceration and release, and that even then an egg was laid on the day of release. In the later periods of broodiness the instinct apparently became progressively more intense.

As a final illustration of the typical cyclical appearance of broodiness the records of hen No. 251, as shown in Fig. 3, may be examined.

In all essential particulars this record is very much like that of hen No. 75 given in Fig. 1. Here the first onset of broodiness was on April 8. After 8 days laying began again; 14 eggs were laid; the second attack of broodiness began May 1. After 10 days laying was once more resumed and again 14 eggs were laid before the brooding instinct made its appearance. Laying began after 9 days and this time 72 eggs were laid. The next period of brooding occupied 9 days (i.e., between laying dates). This case is noteworthy for the evenness of the "clutches" and of the intervening brooding period.

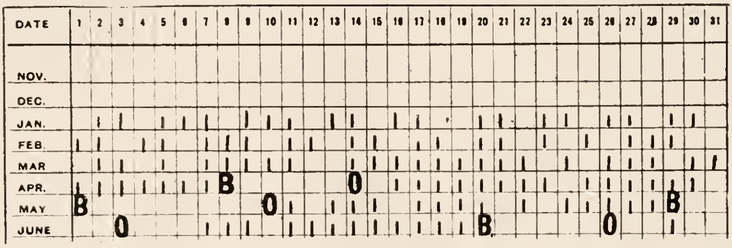


FIGURE 3. Egg record of bird No. 251.

RECURRENCE OF BROODING INSTINCT WITH DIFFERENT DEGREES OF INTENSITY IN THE SAME HEN

From an examination of any large collection of egg record statistics in which broodiness is recorded it will be found that there occur not infrequently individuals in which the instinct to brood is manifested with different degrees of severity at different times, indicating a similar variability in its underlying physiological basis.

An example of this phenomenon is shown in Fig. 4, which gives the record from November 1 to July 1 of bird No. 4.

Here it will be seen that the first period of broodiness began on March 16 and the hen did not again lay until April 2. After laying 4 eggs, she again became broody on April 8, but the period did not last as long as the one before since she was released on April 18 and was laying on the 19th. She did not again become broody until June 14 and this period lasted only 4 days. The bird was released from confinement on the 18th of June and laid an egg on the same day. In this case we have periods of visible manifestation of the brooding instinct lasting 15 days in one case, 10 days in a second case and 4 days in the third case. This certainly indicates a considerable degree of variability in the manifestation of the instinct.

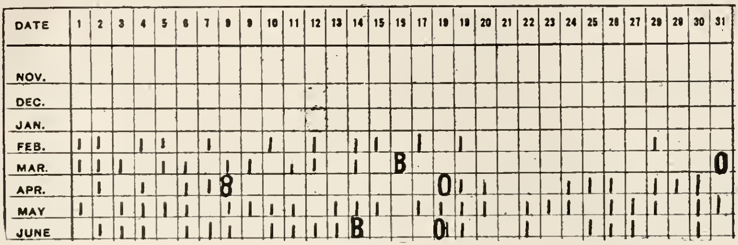


FIGURE 4. Showing the egg record of bird No. 4.

A similar relation is shown in the case of bird No. 444, whose record from November 1 to July 1 is shown in Fig. 5.

This bird was broody at five different times during the period here under consideration. On the first occasion, she was noticed to be broody on January 8, having last laid on January 5. She was released on January 17, but did not lay until February 13, a rest period of 38 days. When she next became broody on March 15, there was an interval without laying of only 13 days.

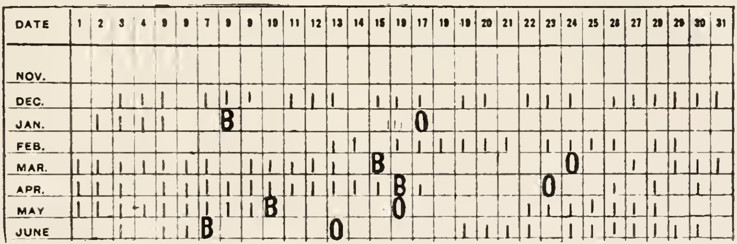


FIGURE 5. Record of bird No. 444.

The rest period of her next broodiness was still shorter. This began on April 16 and lasted but 10 days, on one of which (April 17) the bird laid an egg. The next period of broodiness began May 10. Visible signs lasted 6 days. The whole period during which egg laying stopped was 12 days. Essentially similar relations were shown for the June period of broodiness which began June 7.

These illustrative cases of recurrence of brooding instinct with different degrees of intensity in the same hen could be multiplied many times from our records. There can be no doubt as to the essential fact that the instinct to brood varies in the intensity of its manifestation at different times.

OCCURRENCE OF THE BROODING INSTINCT OUTSIDE OF THE BREEDING OR MATING SEASON

While, as has been seen, broodiness is fundamentally a part of the cyclical series of reproductive phenomena, yet under the more or less artificial conditions of domestication striking changes in its seasonal incidence are frequently to be observed. A hen will go broody at a season of the year when reproduction under normal circumstances would never occur. Furthermore, it often occurs at a much younger age than that at which a bird normally first broods.

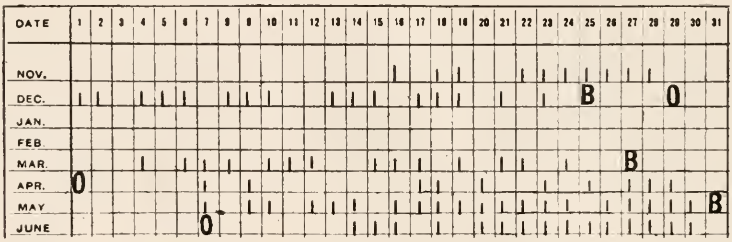


FIGURE 6. Showing record of bird No. 689.

An example of this sort is shown in Fig. 6, which gives the laying record of bird No. 689, from November 1 to July 1.

Here it will be noticed that the bird first became broody on December 25. She did not lay again until March 4 and then again became broody on March 27. It should be said in connection with this record that bird No. 689 was a pullet hatched in the preceding April and was, therefore, at the time when she first went broody roughly eight months old. That this is extremely early for broodiness to occur is shown from general statistics as to the monthly incidence of the first broodiness shown by the individual. During the year for which statistics on this point have been collated there were out of 395 birds which became broody at any time but three that manifested this instinct during the month of December. This is approximately 0.76 per cent. of the flock showing broodiness as early as December. Only 10 of the birds manifested the brooding instinct during the month of January, and 8 in the month of February. Thus all told there were but 21 out of 395, or approximately 5.3 per cent. of the birds which became broody before March 1.

It might be thought that the number of eggs which No. 689 had laid before December 25 was the cause of her going broody at so early a date. As a matter of fact this is not the case because there are many cases (probably hundreds of cases) in our records where pullets laid more eggs than No. 689 during the early winter period and did not go broody at all. A single example may suffice to illustrate the point here. Bird No. 47K laid 106 eggs before February 1 of her pullet year and did not go broody at all. This egg production, it will be seen, is enormously in excess of that of No. 689.

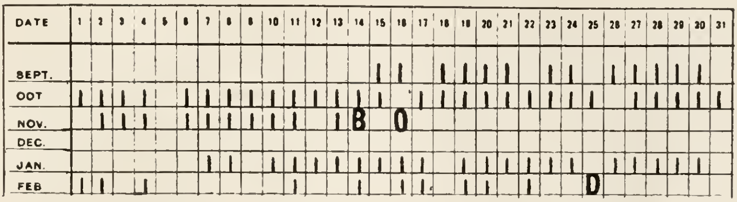


FIGURE 7. Showing the record of bird No. 252-E.

A case of still earlier first broodiness is shown in Fig. 7, which gives the record of bird No. 252E.

This bird was hatched March 31, 1908. She began laying on September 15. She thus began laying when 168 days old. In September she laid 13 eggs, in October 28 eggs, and in November 10 eggs. On November 14 she showed the characteristic behavior of broodiness and was isolated. The symptoms, however, quickly subsided, and she was released on the 16th. The period of rest was protracted until January 7, when she again began laying. She laid through January and less regularly in February up to February 25, on which date she died. In this case the bird first became broody when 228 days old.

Still another case of this sort is shown in the record of bird No. 260E, which is shown in Fig. 8.

This bird was hatched March 31, 1908, and laid her first egg on October 12 at an age of 195 days. In October she laid 13 eggs and in November 7 eggs, going broody on November 9. She was thus at the time of her first broodiness 223 days old. The rest period in this case lasted until December 19, when she began laying again. Before August 1, 1909, at which time she was sold, this bird went broody 6 times, as indicated in Fig. 8. She presents a remarkable record for precocious broodiness, preceded by the laying of only a relatively small number of eggs, namely 20.

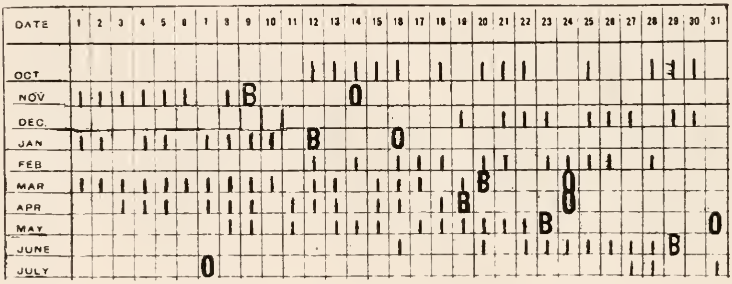


FIGURE 8. Showing the record of bird No. 260-E.

Still a third case of extremely early and frequent broodiness is found in bird No. 380E. This bird was hatched April 15, 1908. She began laying on September 27 at an age of 165 days. She laid fairly continuously, as indicated by the record, up to November 9, when she became broody for the first time. Altogether she produced 29 eggs before November 9. The rest period lasted until January 6, when she began laying again. This bird was only 208 days old at the time of her first broodiness. Like bird No. 260E, she went broody several times in her life; five before August 1, at which time she was sold. This case differs from those already cited chiefly in the fact that the bird was somewhat younger, both when she began to lay and when she first went broody.

BROODINESS NOT PRECEDED BY EGG LAYING OR BY VERY LITTLE EGG LAYING

It was suggested in the preceding section that there was no necessary connection between the number of eggs laid and the manifestation of the brooding instinct. This is very clearly shown by the cases which will be discussed in this section. These are cases in which a bird became broody with little or no antecedent egg production. One of the most striking of such cases in all of our statistics is that shown in Fig. 10, which gives the egg record for bird No. 699 from November 1 to July 1.

It will be seen that this bird went broody on May 10. The only record of egg production before that time is a single egg on November 27. There is every reason to believe that this record of November 27 is an error, probably to be accounted for as an instrumental error of the trap-nest operation. At the time when this record was made the old style trap-nests were in use at this Station. These were in a number of particulars unreliable (cf. for example Pearl [5]). General knowledge of the laws of egg production gained through a number of years study of such matters at this laboratory would indicate with great probability, indeed, practical certainty, that this record was an error. However, if it be allowed to stand, it is clear that it can have had nothing to so with the manifestation of the brooding instinct over five months later. Following this broodiness, bird No. 699 laid an egg on May 29 and another on June 19. These two records are probably correct, since other similar cases are to be found in the Station records. This case proves definitely *that imme-*

DATE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
NOV.																											1				
DEC.																															
JAN.																															
FEB.																															
MAR.																															
APR.																															
MAY										B						0													1		
JUNE																			1												

FIGURE 9. Showing the record of bird No. 699.

diately antecedent laying is not a requisite for the manifestation of the broody instinct.

Similar evidence is afforded by the case of bird No. 130, whose record is given in Fig. 10. This bird became broody on March 16. The records show only one egg before this time to her credit. Whether or not this egg record is an error it is impossible to say. It make no essential difference in the interpretation of the case. Perhaps the most striking feature of this case is the fact that this bird went broody for a second time on April 14, there having been no intervening egg production between the broodiness of March 16 and that of April 14. On May 2 and on May 10 the bird laid an egg. This record essentially confirms the results shown in the case of bird No. 699.

DATE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
NOV																															
DEC																															
JAN.																															
FEB																															
MAR										I						B										O					
APR.														B							O										
MAY		I								I																					
JUNE																															

FIGURE 10. Showing the record of bird No. 130.

The record of bird No. 320 is interesting in this same connection. This record is shown in Fig. 11.

Here there are four distinct and separate manifestations of the brooding instinct between March 25 and July 1. The first period of broodiness began on March 25. Before this time the bird had laid 12 eggs, 11 of them in January and one in March. This egg in March was laid on the 8th and it was 17 days after this before broodiness appeared. It would be extremely difficult to establish any connection between the antecedent laying and the broodiness in this case. On April 19 the bird laid again, this being the first egg since the one of March 8. On April 21 she became broody again, but this was only a mild attack, for she showed visible manifestations on the 24th and laid on the 26th, only to become again broody on the 30th of April. She was released on May 4 and laid May 12 and May 16. The latter of these was her last egg before July 1. Twenty-nine days after this egg was laid, without any intervening production whatever, the bird became broody again on June 14.

The above described observations on normal hens, indicating that the brooding instinct may become manifest without relation to antecedent laying, is supported by experimental work carried on in this laboratory. Such evidence is derived from cases in which the oviduct was completely removed from the bird by a surgical operation, making it impossible for that bird to lay thereafter. Two cases of this sort will be cited here. The protocols of the operations will be given first and then an account of the subsequent behavior of the hens.

Operation No. 34. November 13, 1908. Bird No. 911C. Hatched June 11, 1908. Body weight, 1,480 grams. Under ether anaesthesia[2] the oviduct was completely removed, with the exception of that part of the vagina which is closely attached to the cloacal wall. The left ureter was tied off and cut with the oviduct. All of the ureter, however, was left in the body. The oviduct at the time of the operation was in infantile condition.

DATE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
NOV.																															
DEC.																															
JAN.					I		I		I		I	I		I		I		I		I						I		I			
FEB.																															
MAR.								I																	B						0
APR.																			I		B			0		I				B	
MAY				0								F				I															
JUNE														B						0											

FIGURE 11. Showing the record of bird No. 320.

This bird made an uneventful recovery from the operation. She died and came to autopsy June 14, 1909, that is, 213 days after the operation. The autopsy record is as follows: The oviduct was found to have been completely removed, with the exception of the vagina, which was closely attached to the cloaca. Left ureter had been cut and ligated. It was very much enlarged and filled with a white mass of urates, etc. Evidently the left kidney had almost entirely atrophied. The portion still remaining was covered with a heavy layer of fat. The right kidney had hypertrophied. Remainder of viscera normal.

---

[2] Administered according to the method described by Pearl and Surface (8).

Loose in the body cavity were a number of small irregular shaped hard masses like hardened yolk. These were not enclosed in the peritoneum and showed no decay. Ovary had four or five small absorbing yolks all below one centimeter in diameter. A few small normal yolks (not showing signs of progressing absorption). The body weight at autopsy was 1,995 grams.

While this bird never laid after the operation she frequently went on the trap-nest as though about to lay and was given an "*n*" or nesting record. (Cf. Pearl [6]). On May 28, 1909, this bird showed visible signs of broodiness and was incarcerated. The visible signs of broodiness ceased on June 2 and the bird was released. As has already been stated she died June 14, 1909.

This case demonstrates beyond question that it is not necessary for eggs to be completely separated from the body of the bird (i.e., laid) in order for broodiness to occur. There had, of course, undoubtedly in this case been ovulation into the body cavity from the ovary. This is shown by the fact of record and by the masses of incompletely absorbed yolk found at autopsy.

The second case is of slightly different character, though bringing out the same points. In this operation, the oviduct was not removed but was completely closed near the infundibular end, so that no egg could enter the duct.

The protocol follows.

Operation No. 94. April 16, 1909. Bird No. E490. Barred Plymouth Rock. Body weight 2,220 grams. Under ether anaesthesia the bird was opened. An egg about to be laid was removed from the uterus and a large glass marble was inserted into the oviduct at the mouth of the funnel. The funnel mouth was then completely closed with a series of closely spaced stitches, making it impossible for anything to leave or enter the oviduct at that end. The bird made an uneventful recovery from the operation.

This bird, of course, never laid after the operation, but on July 24 she became broody and continued with visible manifestations until July 27, at which time she was released. Prior to the operation, the bird's laying record had been as follows: In January she laid 2 eggs, in March 13 eggs, in April 6 eggs before the date of operation. She had never been broody before the operation, but, as already stated, did become so on July 24 without any antecedent laying.

A change in the order of events in the cyclical processes of reproduction is well known for other birds. While normally broodiness follows a period of laying, it does not always do so, even in other birds than the domestic fowl. Replying to an inquiry regarding this point in pigeons, the late Professor C. O. Whitman wrote me on October 22, 1909, as follows: " You ask whether in pigeons broodiness ever occurs without the laying of eggs. I have had such cases in different species many times. For example, a pair of Pouters, hatched last year, have repeatedly built a nest this summer without laying any eggs and yet have incubated the empty nest in quite regular order, the male and female alternating in sitting."

Similar disturbances of the normal sequence of events in the reproductive cycle of mammals are not unknown. I might cite here by way of illustration a case of appearance of heat in a mare shortly before parturition (Bell, [1]). He says:

" The thorough-bred mare, Lady Gower, foaled on April 12. The foal was a very small one, and only lived for a short time. During the period of utero-gestation there was nothing to call for remark until March 5th, five weeks before the mare was delivered of the foal. On this date the symptoms of oestrum were most marked, and she was put to the horse, no suspicion being then entertained that she was in foal. What is still more remarkable, however, is the fact of the recurrence of oestrum on April 7 and April 11, on both of which dates the mare was served, parturition taking place the day after the last service."

THE BROODING INSTINCT MANIFESTED WITH A VERY SLIGHT DEGREE OF INTENSITY

It is not infrequently found to be the case, especially with birds which are good layers, that well defined brooding behavior may appear, only to disappear very quickly under the confinement treatment. Such cases indicate that either the original intensity of the instinctive behavior was slight or else it was very quickly aborted.

Records of this kind are shown in Figs. 12 and 13.

Fig. 12 gives the record of bird No. 401 from November to July 1. It will be seen that this bird was a fairly good winter layer. She showed no signs of broodiness until May 6, when she very clearly gave the manifestations of broodiness, and was, on that account, incarcerated. The symptoms, however, quickly subsided. She was released on May 9 and laid an egg the same day.

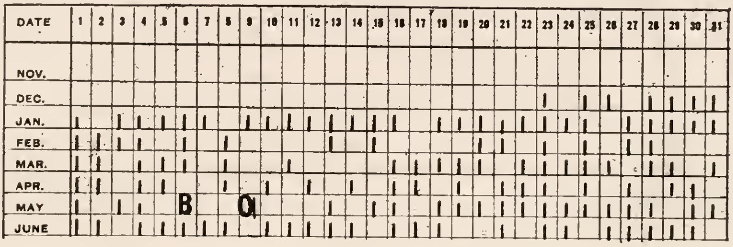


FIGURE 12. Record of bird No. 401.

The record of bird No. 408 almost parallels this, the chief difference being in respect of the time at which broodiness appeared. In the case of No. 408 it was on May 23, and was clean-cut and definite. The manifestations, however, quickly disappeared. On the 27th the bird was released, and laid an egg the same day.

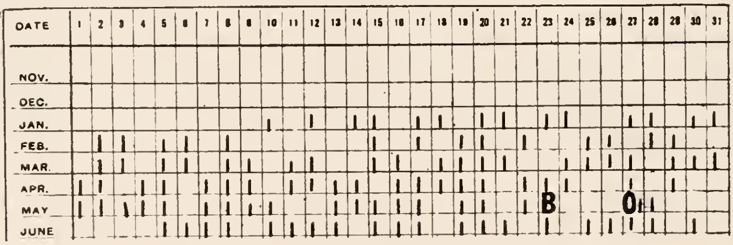


FIGURE 13. Record of bird No. 408.

DISCUSSION

In this paper I have tried to bring together some of the facts regarding broodiness in fowls which appear clearly when one collects extensive and accurate statistics on the matter. The essential purpose of this paper is to define the problems which need further physiological analysis rather than to solve them. The data presented in this paper are facts which any theory of the physiological basis of brooding behavior must take into account.

In the present state of knowledge the physiological cause or basis of the phenomenon known as broodiness, which every bird shows in one form or another, is not at all clear. From the facts set forth in this paper it is obvious that broodiness is a much more variable phenomenon than oestrus in mammals. In the first place it lacks entirely the regularity of the occurrence of oestrus. Even in the cases where periods of broodiness do recur rather regularly (cf. Figs. 1, 2, and 3) it is clear that we have nothing like the regularity of the dioestrous cycle of mammals.

It is furthermore certain that brooding is not a necessary or essential element in the reproductive processes in the domestic fowl, in the sense that any other element in the cycle is dependent upon it as a necessary antecedent. Some hens which lay perfectly well throughout their lives, and whose eggs produce perfectly normal healthy chickens never manifest the slightest indication of the brooding instinct.

It appears to be the case that in the domestic fowl the brooding instinct has to a very large degree disappeared along with the fact of domestication. This is particularly true in the case of fowls which have been systematically bred for a considerable period of time for high egg production. In such strains it is difficult to find fowls in which the brooding instinct is sufficiently strong to last out the 21 days necessary to hatch eggs. Here we have repeatedly tried during the last six years to get broody Barred Plymouth Rock hens to hatch eggs. Only in extremely few cases has it been possible to do this. In most cases the bird will sit for a while, then cease all manifestations of the instinct and begin laying again. It seems highly probable that broodiness is in some way dependent upon factors which are inherited in a Mendelian manner. A large amount of material has been accumulated regarding this point and it is hoped that the analysis of it will soon be completed.

It would seem that broodiness is rather directly connected physiologically with the functioning of the ovary. That it is not connected with the functioning of the oviduct is clearly demonstrated in the present paper by the cases in which the oviduct is removed, or put into a non-functioning condition. In these cases, however, the normal functioning of the ovary had in no wise been interfered with. It is an interesting fact in this connection to note that birds in which the ovary is non-functional never show manifestations of broodiness. Evidence on this point is found in cases of incomplete hermaphroditism such as that described by Pearl and Curtis (7). In the case referred to, the bird, No. 16D, had a non-functional ovary. Her record shows that she never manifested the slightest signs of broodiness. Still more striking evidence is afforded by the case of bird No. 8051, which was described by Pearl (6). This bird had an ovary which was apparently entirely normal, but remained throughout life in an infantile condition. This bird was hatched on March 29, 1909, and died August 24, 1912. During the whole life she never visited the nest, or showed in any way the slightest manifestations of broodiness. A photograph of the ovary of this bird is given in the paper cited. This is apparently a case of a normal but non-functional ovary and no broodiness occurred.

Interesting light has recently been thrown on the question of the physiological condition of a brooding bird by the very thorough and extensive investigation of Gerhartz (2). This author shows that the state of broodiness is one of profound physiological rest or depression. He says: (*loc. cit.* p. 44).

" Der Netto-Energieverbrauch für die auf dem Nest sitzende Bruthenne ist ausserordentlich niedrig: 53.4 Cal. pro Kilogramm Korpergewicht und Tag. In derselben Periode liegt der Energieverbrauch bei der night sitzenden, aber sich doch sehr ruhig verhaltenden Henne ebenfalls sehr niedrig: bei 74 Cal. Geht man von dem erstgenannten Minimalwert aus, so zeigt sich, dass der Energieverbrauch beim Huhn, das in normaler Ruhe ist und sich in einem geraumigen Käfig aufhalt, im allgemeinen um 59.5% des Minimalwertes höher liegt (Plus von 31.73 Cal. pro Kilogramm und Tag), in der Mauserperiode aber gar der pro Kilogramm und Tag erforderliche Energiebetrag um 84% des Minimal wertes steigt, also fast den doppelten Wert erreicht. In der Legeperiode erhoht sich der Bedarf um fast das Dreifache."

This discovery that the brooding state is one of physiological depression is somewhat contrary to the common belief of poultrymen, who have usually supposed that broodiness indicated a condition of unusual physiological excitation. The precise measurements of energy metabolism which Gerhartz has given are, however, conclusive. It is not clear, from the behavior standpoint, what the relation is between the manifestations of the brooding instinct, and the physiological state of the bird. In this connection it may be noted that it frequently happens that a bird will exhibit periods of rest in egg production, which are as long continued as those of broodiness, and yet show none of the objective features of broodiness whatsoever. Such cases prove that the cessation of ovarian activity (laying) is not *alone* capable of causing the onset of broodiness. It would be extremely interesting to have more extensive data as to energy consumption in these birds which are not laying, and yet are not manifesting the broodiness instinct.

In the fowl, broodiness seems to be distinctly a female secondary sexual character. This, of course, is not true in some other species of birds where the male bird alternates with the female in brooding eggs. Ordinarily in the domestic fowl the cock takes no part whatever in the brooding of the eggs or the chicks. It has, however, long been the practice with practical poultry keepers in certain parts of the world to use the castrated cock or capon for the purpose of brooding chickens. I know of no record of capons being used to incubate eggs. The brooding behavior of the capon needs, and will certainly repay, careful study by a trained behaviorist.

SUMMARY

This paper presents data regarding variations in the manifestations of the brooding instinct in fowls. It is shown that:

1. Broodiness normally constitutes one element in the cyclical reproductive activities of the female. It recurs with greater or less regularity following periods of laying.
2. The degree of intensity of the brooding instinct, both in respect of its objective manifestations and in respect of its physiological basis, may vary considerably at different times in the life of the same individual.
3. Broodiness in the domestic fowl is not necessarily connected with any particular season. It may occur entirely outside the regular breeding season.
4. While ordinarily broodiness is preceded by the laying of a " clutch " of eggs, this need not necessarily be so. Cases are cited in which well marked broodiness occurs without antecedent laying.

5. Well marked broodiness behavior may in certain cases disappear very quickly.

6. The manifestations of the brooding instinct are apparently closely connected with the functional activity of the ovary, though the precise nature of the connection has not yet been analyzed.

LITERATURE CITED

1. Bell, R. Appearance of Oestrum in a Mare Shortly Before Parturition. 1880. *Veterinarian*, Vol. LIII–Vol. XXVI, Fourth Series, p. 331.
2. Gerhartz, H. Ueber die zum Aufbau der Eizelle notwendige Energie (Transformationsenergie). 1914. *Pflüger's Arch. Bd.* 156, pp. 1–224.
3. Herrick, F. H. Analysis of the Cyclical Instincts of Birds. *Science, N. S.*, 1907. Vol. XXV, pp. 725–726.
4. Herrick, F. H. The Blending and Overlap of Instincts. *Science, N. S.*, Vol. 1907. XXV, pp. 781–782.
5. Pearl, R. On the Accuracy of Trap Nest Records. *Ann. Rept. Me. Agr.* 1911. *Expt. Stat. for* 1911, pp. 186–193.
6. Pearl, R. The Mode of Inheritance of Fecundity in the Domestic Fowl. 1912. *Jour. Exper. Zool.*, Vol. 13, pp. 153–268.
7. Pearl, R. and Curtis, M. R. Studies on the Physiology of Reproduction in the Domestic Fowl. III. A Case of Incomplete Hermaphroditism. 1909. *Biol. Bul.*, Vol. 17, pp. 271–287.
8. Pearl, R. and Surface, F. M. The Use of Atropin Sulphate in Anaesthetizing 1909. Birds for Surgical Experiments. *Jour. Amer. Med. Assoc.*, Vol. 52, pp. 382–383.
9. Tegetmeier, W. B. The Poultry Book. *London.* 1867.

NOTES

ON THE THELE-PERCEPTION OF SEX IN SILKWORM MOTHS

PROFESSOR OSV. POLIMANTI
The Physiological Institute of the University of Perugia

While carrying on a series of researches on the caterpillar of *Bombyx mori* L.,[1] my attention was attracted by a phenomenon presented by the male moth just after emerging from the cocoon. The moth began to move its wings very rapidly while clinging with its feet to some one of the still unopened cocoons, and it remained thus even after the moth from that cocoon had emerged. It occurred to me that this might be due to the fact that the unopened cocoon held a female, to which the male was guided by some peculiar scent. After postponing for several years any attempt to prove the truth of this supposition, I have at last made some systematic observations which are here recorded.

It has long been noticed by naturalists that the male moths of the Bombicidae, immediately on emerging from the cocoon, seek out the female, guided, it is supposed, by the sense of smell. The wings of the female are not well developed, and they seldom fly far; the males, on the other hand, may make real migrations in search of the female.

It is also well known that certain moths emanate peculiar odors. The seat of the odor was shown by Fritz Müller[2] to be small blades provided with a gland at the base, situated in the superior part of the anterior wings near the junction with the thorax. To these he gave the name "Andraconia." He described the odors of a large number of moths and butterflies, some of which were pleasant and others disagreeable. Müller considered these odors a means of sex attraction. Leoni, however, found them present in both males and females and interpreted them as a means of recognition among individuals of the same species.

---

[1] Polimanti, O. Contributi alla fisiologia del baco da seta (*Bombex mori*) Scansano. Tessitori. 1906. Contributions à la physiologie de la larve du ver a soie (*Bombyx mori*). *Archives italiennes de biologie.* T. **47.** 1907. P. 341-372.

[2] Müller, Fritz. 1. Wo hat der Moschusduft der Schwärmer seinen Sitz? Kosmos. 1878. 2 v. 3. p. 84. 2. Duftbüschel von Sphingiden. *Transactions Entomological Society,* London. 1878. P. 2.

Fabre[3] carried on some experiments, to determine this point, with *Saturnia pyri* and *Gastropacha quercus.* He placed a female of Saturnia in a cage of wire netting. During the night the cage was surrounded by males of the same species. To ascertain whether it was by means of the antennae that the odor was perceived by the males, he cut off their antennae and moved the female to another room. On the following night only one of these males with amputated antennae was found in the number which flocked around the cage. This fact might be due, however, to the short life of the adult male. In all, Fabre captured, during eight evenings, one hundred and fifty males, which was the more remarkable because very few individuals of this species had been known in that vicinity, and very few cocoons had been found. Some of the moths must have come long distances. Fabre explained the phenomenon by the existence of emanations insensible for us but capable of influencing an olfactory sense more acute than ours. He experimented also with receptacles, for the female, of different materials, of tin, wood and pasteboard, and found that only when these were hermetically sealed did the males fail to find the female. Nor did the attempt to mask the odor by means of other strong odors, like those of naptha, essence of nard, petroleum, carbon disulphide, have any different result. When the female was placed under a glass shade, the males paid no attention to her, but hovered around the cage in which she had previously been confined. In this last experiment, it became evident that sight had nothing to do with attracting the males. These experiments were repeated later by Fabre with Bombyx.

The experiment of cutting off the antennae of the oak eggar (*Gastropacha quercus*) gave doubtful results. The grass eggar (*G. trefolii*) showed less acuteness in discovering the female. The existence of a special odor in the female of Saturnia and *Gastropacha quercus* was, however, thoroughly established by Fabre's experiments. How these odors are perceived remains to be solved. It is difficult to imagine any substance which, according to physical and physiological laws, could be so diffused as to be perceptible at a distance of many kilometers; and just as extraordinary must be the sense which serves to discover it. Fabre is right in observing that the world of sensations is much wider than our imperfect and obtuse organs of sense reveal to us. It is now certain that animals, for instance, hear sounds that escape our ears; see ultra-violet rays which our eyes do not see. It is easy to believe that these lower organisms, especially the insects, are endowed with organs of sense quite special and so complicated that they differ absolutely from ours. They may serve purposes as different from any of ours as sound, for instance, differs from light. It is only by indirect methods, that is, by the study of ethology, of the intelligence of animals, of their relation to the forces of nature, of the appearance which the external world has for them, that we can arrive at the discovery of the senses and sensations which are now only an hypothesis.

---

[3] Fabre, J. H. Souvenirs entomologiques. Paris. T. 4. P. 56.

Another characteristic of the *Bombyx mori* which I studied, and also of other moths, is the buzzing made by the wings. In the males of Bombyx, this is more intense than in the females, and the movements of the wings are more rapid. The movements are more rapid also when the male is resting upon a cocoon which contains a female moth about to emerge, than when it rests upon any other object. In this case, the male may hear the movements of the female inside the cocoon, and having thele-perception of the sex, augments the vibrations of his wings.

In performing my experiments, I took two hundred cocoons of *Bombyx mori* and kept them in a big pasteboard box at a constant temperature of 15° C. As the moths emerged, I recorded whether they attached themselves at once to another cocoon, whether they remained there constantly until the enclosed moth came out, and whether the latter was of the same or different sex. I reckoned also the uncertain results, that is, the cases where the moth did not remain constantly on one cocoon, but went to another from which afterwards came a moth of the same or different sex.

TABLE

Summary of Experiments

No. of moths ♂ attached to cocoons from which came moths ♀ and quantity %	No. of moths ♂ attached to cocoons from which came moths ♂ and quantity %	No. of moths ♀ attached to cocoons from which came moths ♂ and quantity %	No. of moths ♀ attached to cocoons from which came moths ♀ and quantity %	No. of moths ♂ or ♀ attached successively to cocoons from which came moths ♂ or ♀ and quantity %
85 (42.5%)	77 (38.5%)	8 (4%)	0	30 (15%)

From this table it is evident that the greater number of the males of *Bombyx mori* soon after emerging from the cocoon attached themselves to cocoons from which afterward came female moths. A large number, however, attached themselves to cocoons from which came male moths; only a small number of females attached themselves to cocoons containing male moths, and none to those holding female ones. Lastly, a number (15)% of both males and females attached themselves successively to cocoons containing moths of one sex or the other. These are, in short, individuals uncertain of their choice and which, of course, we cannot take into account in these experiments because they do not forward our conclusions.

I have observed, further, that when a moth, either male or female, attaches itself to a cocoon from which later emerges a moth of either the same or different sex, it produces always the same number of vibrations of the wings; that is to say, whatever may be the sex of the moth in the cocoon, the free moth causes its wings to vibrate in that given and determinate rhythm with the certainty that there is in the cocoon an individual of the opposite sex.

From these experiments we may concluded that the theleperception of sex (olfactory?) in the moth of *Bombyx mori* is not well developed. The membrane of the cocoon may oppose too great an obstacle to the characteristic olfactory vibrations which come from the female. It seems, then, that such a membrane is enough to prevent such vibrations.

A NOTE ON THE PERSISTENCE OF AN INSTINCT

K. S. LASHLEY

Ordinarily the nursing instinct in young mammals is very transitory, being readily suppressed and superseded by the developing habits of obtaining food in other ways, and with its disappearance the co-ordinated group of reflexes involved in sucking seems in many species to be completely lost. In the case of man, however, recent investigations indicate that the persistence of this instinct in some perverted form into adult life is by no means uncommon. This brings to the front the question of the existence of a similar condition in animals. The following observations upon the continuation of the sucking reflexes into the adult life of the cat may be of interest in this connection, although little insight into the causes of the behavior has been obtained.

The first case of this sort, coming to my attention some years ago, was that of an adult male cat (J), two years old, which persisted in sucking at the fur and skin of other cats, pets in the same household. The cats were accustomed to lie together in the sun or before the fire, washing each-other's faces and exchanging other amities. In such friendly overtures J was particularly active, but he always ended his ministrations by first licking the fur of his companion's throat until it was thoroughly wet and then applying his lips to the exposed skin and sucking vigorously. If uninterrupted he would lie thus for hours and if he were pulled away suddenly, a faint oozing of blood was generally visible on his companion's throat where his lips had been applied. Since the behavior was somewhat detrimental to the other cats it was broken up by the application of Cayenne pepper to their throats.

The second case is more interesting since a little of its history is known. In the summer of 1913 a kitten was taken from her mother before she had learned to drink and for several days was fed by hand, sucking at bits of rag soaked in milk. She was given an old piece of fur as a bed and spent much of her time nuzzling about vainly among its hairs. Four months later, when I saw her for the second time, she had developed a very pronounced habit of sucking at small objects. She would lie for half an hour at a time and suck at the tassels of a heavy woolen curtain, making loud smacking and gurgling noises and refusing to be distracted by food or even by mild punishment. The taste of the object was seemingly not the source of attraction for a bit of undyed thread, one's finger-tip, or even the cap of a fountain pen served as a ready substitute for the more favored tassels. Even threads moistened with weak sugar, salt, and acid solutions were accepted, although such solutions usually produce violent avoiding reactions in normal cats. Hunger was not instrumental in producing the activity, which frequently appeared just after the kitten had eaten a full meal. I have not been able to secure this animal for further observation but am informed that her peculiar behavior is still unchanged. (She is now nearly a year old.)

This behavior is, at least on the surface, strikingly like the "pleasure sucking" described by students of human behavior. The existence of complex perversions in animals, as suggested by these cases and by Pearl's recent note upon the behavior of the Poitou jacks,[1] offers a possibility of the application of animal behavior studies to man, particularly with respect to the experimental study of the rôles of heredity and environment in the development of character, which it will be well to bear in mind in the more general studies of habit formation.

---

[1] Pearl, Raymond. Note on the sex behavior of the Poitu Jacks. *Jour. Animal Behavior.*, vol. 3, 297-299.

JOURNAL OF ANIMAL BEHAVIOR

VOL. 4 SEPTEMBER-OCTOBER, 1914 No. 5

A STUDY OF SEXUAL TENDENCIES IN MONKEYS AND BABOONS

G. V. HAMILTON
Montecito, California

In spite of the considerable advance that has been made in our knowledge of sexual life since the appearance of Freud's (1) *Drei Abhandlungen zur Sexualtheorie*, we still lack that knowledge of infra-human sexual life without which we may scarcely hope to arrive at adequately comprehensive conceptions of abnormal human sexual behavior. For example, the possibility that the types of sexual behavior to which the term "perverted" is usually applied may be of normal manifestation and biologically appropriate somewhere in the phyletic scale has not been sufficiently explored. Homosexual tendencies come to frequent expression in adolescent boys and girls, thereby presenting to the mental hygienist a problem, the solution of which awaits, first of all, biological knowledge of homosexuality which only the behaviorist can supply. It is unnecessary to multiply examples in illustration of the fact that both the theoretical interests of the science of behavior and the practical needs of what we may regard as a group of applied sciences of human behavior (viz., mental hygiene, criminology, psychopathology) place upon the animal behaviorist an obligation to lay the necessary foundations for a scientific and thoroughly comprehensive investigation of sexual life.

The above considerations, of which I have been almost daily reminded by clinical contacts with human sexual problems, have led me to formulate the following problems in animal behavior:

(1) Are there any types of infra-human primate behavior

which cannot be regarded as expressions of a tendency to seek sexual satisfaction, but which have the essential objective characteristics of sexual activity ?

(2) Do such sexual reaction-types as homosexual intercourse, efforts to copulate with non-primate animals and masturbation normally occur among any of the primates, and if so, what is their biological significance ?

It is always a difficult matter to collect scientific data which shall be specifically relevant to behavior problems when such problems do not lend themselves to strictly experimental methods of investigation. Even under carefully prearranged experimental conditions one cannot always be sure that adventitious stimuli may not have played a part in bringing about a given response. This uncertainty is much greater when the animal subject is either at large with his fellows or confined with them in a cage of sufficient size to allow a reasonable approximation to natural conditions. Under such circumstances the best that one can do is to supply a set of conditions which are apt to lead to a fairly definite and uncomplicated development of the desired situation.

The monkey's marked variability of response presents a further difficulty, for in seeking to identify a definite situation-response sequence the observer is called upon to distinguish activities that are essential components of a given reaction-type from purely fortuitous activities. For example, in a given case a monkey's manipulation of his genitalia may be nothing more than reflex scratching of a momentarily irritated area, and not at all a part of his response to the situation of which the observer wishes to determine the reactive value. In many cases I have been unable to ascertain the essential components of a given reaction-type until prolonged contact with my subjects has enabled me to predict with reasonable certainty that whenever the appropriate situation developed a sequence of activities composed of such and such members would be manifested.

A difficulty of another kind is encountered when one seeks to present results that have been obtained by non-experimental methods. Such results can seldom be indicated by tables of figures, habit-formation curves, etc., because reaction to "natural" situations are usually complexes of activities which call for detailed description. When, as in the present instance, the observer arrives at conclusions which have no value unless they are found to be justified by the facts upon which they are based, and when the presentation of all the facts involved would require the space of several printed volumes, some method of abridgment must be adopted. An abridged journal is not apt to be satisfactory where an extensive program of observation has been followed unless, as rarely happens, the most convenient and logical order in which the facts can be presented coincides with the order of their occurrence. I have followed the order of presentation outlined below for the sake of effecting a satisfactory abridgment without resorting to the awkward expedient of publishing extracts from my note books in journal form:

I. List of subjects.
II. Description of environmental conditions.
III. A list of the types of situations that were arranged by the observer or encountered by the subjects in consequence of their spontaneous activities; and under each description of a typical situation one or more detailed descriptions of typical responses thereto.
IV. Classification of reactions as expressions of reactive tendencies.

I. DESCRIPTION OF SUBJECTS

The estimated or known age of each subject is given for January, 1914. Inability to identify an animal as to species is indicated by a dash after the generic name. The "pet" name of each animal is given to facilitate the reader's identification of subjects in subsequent descriptions of behavior. An animal's sex is indicated by its laboratory number—even numbers for males, odd for females. In reporting the behavior of an animal the first reference to it will include, in the order given, its laboratory number, pet name and initial letters of the genus and species to which it belongs. E.g., "7-Becky-M-r" refers to Monkey 7 of the list, and indicates that she is a female *M. rhesus.*

Monkey 1. Bridget. *M. rhesus.* Adult.

Monkey 2. Mike. M. adult. About 1/4 larger than adult male *M. rhesus.* Fur grey and luxuriant. Tail about 8 centimeters long and furred to the tip. Body thick, face broad. Readily identifiable as a macaque.

Monkey 3. Kate. *M. rhesus.* Adult. Mother of Monkey 9.

Monkey 4. Pat. *M. rhesus.* Adult. Vision defective.

Monkey 5. Maud. *M. rhesus.* Young adult.

Monkey 6. Jocko. *M. cynomolgus.* Adult.

Monkey 7. Becky. *M. rhesus.* Adult. Mother of Monkeys 13 and 24.

Monkey 8. Jimmy I. *M. cynomolgus.* Adult.

Monkey 9. Gertie. *M. cynomolgus-rhesus.* Age, 3 years, 2 months. Daughter of monkeys 3 and 10. First pregnancy began September, 1913.

Monkey 10. Timmy. *M. cynomolgus.* Adult. Father of Monkeys 9, 13 and 24.

Baboon 11. Grace. *Papio*—. Adult. A small black baboon, about 1-3 larger than an adult female *M. rhesus.* Tail absent, other anatomical features similar to those of typical members of genus *Papio.* Became pregnant when bred to male baboon (Monkey 12) but frequent previous copulation with male macaques was without result.

Baboon 12. Sandy. *Papio*—. Adult. Fur black over back and forehead, grey elsewhere. " Pig " tail, long muzzle. Legs and body much shorter and thicker and those of the chacma. A very powerful animal, almost equal to the chacma in weight.

Monkey 13. Tiny. *M. cynomolgus-rhesus.* Age, 5 months. Daughter of Monkeys 7 and 10.

Monkey 14. Jimmy II. *M. cynomolgus.* Young adult.

Monkey 16. Sobke. *M. rhesus.* Young adult.

Monkey 18. Baby. *M. cynomolgus.* About 1-2 adult size. Castrated before sexual maturity.

Monkey 20. Chatters. *M. cynomolgus.* About 3-4 adult size. Castrated before sexual maturity.

Monkey 22. Daddy. *M. cynomolgus.* Adult. Castrated—date unknown.

Monkey 26. Skirrel. *M. cynomolgus.* Adult.

Monkey 28. Scotty. M—. Young adult. Probably belongs to the cynomolgus group.

II. ENVIRONMENTAL CONDITIONS

My laboratory is in the midst of a live oak woods in Montecito, California, about five miles from Santa Barbara. Like all of

Southern California, Montecito is not entirely free from frost, but the winters are so mild that when the orange and lemon growers far to the south of us are compelled to use artificial heat in their orchards to prevent damage by frost, our local growers find it unnecessary to take any precautions whatsoever against the cold. The climate here is therefore exceptionally mild, even for Southern California, and at no times seems to reduce the activities of macaques—except, of course, when rain drives them to shelter. My subjects have always been in excellent physical condition, the only deaths having been due to accident or to pathological causes that were operative at the time of an animal's purchase.

In front of the laboratory is a quadrangular yard, 16.7 meters long by 7.4 meters wide. The laboratory encloses one end of this yard, and the cage one side. The other end and side of the yard is enclosed by a solid board fence which is 1.9 meters high. The entire enclosure is surrounded by live oak trees, and one tree is contained within the yard. The animals, when at large, could wander to an indefinite distance from the laboratory by passing from tree to tree, but they rarely wander out of sight of the yard.

The cage is 6 meters high, 16.7 meters long and 1.8 meters wide. The front, top and upper half of the rear and ends are covered with wire netting, the meshes of which are 1.4 centimeters square. The lower half of the rear and ends is solidly boarded, to give stability to such a tall, narrow structure. The cage is subdivided into eleven compartments by partitions of which the lower one third is wood and the upper two thirds wire netting (1.4 cm. mesh). Within 72 centimeters of the top of each compartment is a horizontal shelf, 30 centimeters wide. Each compartment is also equipped with a sleeping box, a food drawer, and proper drainage for the concrete floor. A door at the rear gives access to the man who cleans the cage.

An important accessory to the cage is a wooden alley, which extends along the entire rear of the structure, midway between the top and bottom. This alley is 75 centimeters high by 60 centimeters wide. Each compartment opens into the alley by means of a sliding door arrangement, which enables the observer to make it accessible to the occupants of one or more compartments, according to the demands of a given experiment.

III. TYPES OF SITUATIONS AND OF RESPONSES THERETO

The outdoor conditions described above have enabled me to liberate most of the subjects in selected pairs or groups. 13-Tiny-M-cr was too young, and 10-Timmy-M-c, 12-Sandy-Papio—, 26-Skirrel-M-c and 28-Scotty M— were too large to be safely liberated, but an excellent substitute for outdoor freedom was obtained for them by giving them access to the long alley and three or four of the cages. I have been able to form a fairly accurate estimate of the effects of cage-life on sexual behavior by comparing the activities of animals that have been at large for several months with the activities of those that have been continuously confined. At this point it may be said that, provided the macaque or baboon have a sufficiently wide range for pursuing and fleeing his enemies, playing with his fellows, etc., confinement will be found to have no perverting effects in this climate.

In the following list of observations I have endeavored to spare the reader the inconvenience of being compelled to make frequent reference to the list of subjects by giving in each instance the age of the animals under discussion, rather than the date of the observation. Wherever reference is made to an animal as " sexually immature " it is to be understood, in the case of females, that menstruation has not yet appeared; males are regarded as sexually immature until they have assumed the characteristic strut that I have found to be coincident in appearance with seminal discharge on copulating with females. Sexual maturity, in this sense, antedates the attainment of adult size by at least a year.

Situation 1. Male and female separated from one another (but not from fellows of the opposite sex) for at least one week, then given access to one another.

Observation 1. 10-Timmy-M-c and 5-Maud-M-r, both sexually mature, occupied separate cages, each with a mate, for several weeks. Each animal had been copulating freely. They were then given access to one another, their respective mates having been tolled into an empty cage and confined therein. Timmy rushed from the alley into Maud's cage as soon as her door was opened. She observed his approach from her shelf, and as he ascended toward her, smacking his lips, she, too, smacked her lips. As soon as the male clambered upon the shelf the female assumed the sexual position, viz.: Hind legs fully extended to an almost vertical position; forelegs sharply flexed; tail erect; body inclined forward and downward from the hips; head sufficiently extended and rotated to enable the female to direct her gaze upward and backward. The male grasped the female at the angles formed by the juncture of hips and body with a hand on either side, and in mounting her, he clasped her legs just above the knees with his feet. He leaned forward and downward during copulation, smacking his lips violently. The female seemed to invite contact with his mouth, for she persistently thrust her smacking lips towards the male, until he leaned still further downward and touched her lips with his own. Shortly before copulation ceased, the male uttered a succession of shrill little cries, and greatly increased the vigor of his copulatory movements. As soon as he dismounted the female, he took her tail in one hand and elevated it, then with his free hand examined her vaginal labia, at the same time closely inspecting them with nose and eyes. Then he lay down and the female examined his fur "flea-hunting."

Observation 2. 11-Grace-Papio— (sexually mature), 14-Jimmy-M-c (sexually mature), the three eunuchs and a number of immature monkeys had been at large for several weeks. Grace had freely copulated with all of the males, including the eunuchs. 16-Sobke-M-r (sexually mature) had occupied a cage with a mature female for several weeks. He was now liberated. As soon as he and Grace caught sight of one another they began smacking their lips. Their subsequent behavior was essentially similar to that of the animals described in observation 1.

Situation 2. Male and female after several days' access to one another, during which copulation had been of frequent occurrence.

Observation 3. After Timmy and Maud had been together one week (date of this observation is one week later than that of observation 1, q.v.) Timmy was offered a loquat. He descended from his shelf, leaving Maud still perched upon the shelf. As soon as he had reached the floor, and had received and eaten the loquat, he began to stalk his mate, slowly ascending with tail erect, gaze fixed upon the female, and head jerked forward now and then as if to threaten violence to Maud. Such behavior often precedes an attack upon another male. When he finally attained the shelf he copulated with Maud in the manner described in observation 1. After a few minutes he again mounted her, but this time the female merely arose from a crouching to a quadrupedal standing position, without displaying signs of sexual excitement. There was no smacking of lips by either animal, and the desultory efforts of the male to copulate terminated as soon as he entered the female and made two or three strokes. Both animals sat inactive for five minutes, then the male drew the female's hind quarters towards him. He started to mount, then desisted and began to inspect her genitalia with eyes, nose, mouth and fingers. After two or three minutes of this behavior he copulated, both animals displaying sexual excitement. During the next half hour there was an alternation of perfunctory attempts at copulation with more vigorous attempts, the latter being immediately preceded by examinations of the female's genitalia on the part of the male.

Observation 4. 14-Jimmy II-M-c and 9-Gertie-M-cr (both sexually mature young adults) had been at large together in company with a number of other males and females for several weeks. They had copulated a number of times each day. Their behavior during a half hour when they were perched together upon the roof of the laboratory consisted in the same alternation of perfunctory attempts at copulation with more vigorous attempts, the latter being immediately preceded by examination of the female's genitalia on the part of the male. Jimmy II is more apt to follow me about when he is at large than to stay with the tribe, and this may account for the fact that he manifested the behavior just described less frequently than did Timmy. 26-Skirrel-M-c manifests such behavior more frequently than does Jimmy II and less frequently than does Timmy. The mature rhesus male (16-Sobke-M-r) also inspects the female's genitalia after a perfunctory attempt at copulation and just before a vigorous attempt, but he is more apt to increase his sexual excitement by chasing and biting the female. All of my mature males, with the exception of the eunuchs and the baboon, at times chase and bite their mates in apparent preparation for copulation, but only after prolonged access to them.

Situation 3. Two males, confined in separate cages with mates, are caused to exchange mates.

Observation 5. 16-Sobke-M-r and 3-Kate-M-r (both sexually mature) had occupied a cage adjacent to that occupied by 10-Timmy-M-c and 11-Grace-Papio— (both sexually mature). The males had ceased to copulate vigorously with their mates without first examining their genitalia or chasing and biting them. When Timmy was now separated from Grace and put into Kate's cage—Sobke having previously been removed—he dashed up the side of the cage toward Kate and copulated with her vigorously without any preliminary attentions to her. The female displayed sexual excitement, although she had ceased to do so when copulating with Sobke unless he first examined her genitalia or chased and bit her.

As soon as this observation was completed, Sobke was allowed to enter Grace's cage. He, like Timmy, had ceased to copulate vigorously unless he first examined or chased the female. But as soon as he was given access to Grace he displayed great sexual excitement, and copulated vigorously, without having engaged in any preliminary activities conducive to sexual excitement. After a few days the behavior of the newly mated couples toward one another was essentially similar to their behavior toward their former mates. When they were restored to their former mates, vigorous copulation again ensued without preliminary examining and chasing on the part of the males.

Situation 4. Female taken from her mate and given to a male in an adjacent cage, her mate being left alone in his cage.

Observation 6. 10-Timmy-M-c and 11-Grace-Papio— had occupied a cage together for several weeks, and 26-Skirrel-M-c had been alone in an adjacent cage. All subjects were sexually mature. Grace was taken from Timmy and given to Skirrel. As soon as Skirrel began to copulate with Grace on the shelf of their cage Timmy, who was on his shelf and therefore in very close proximity to his former mate and to Skirrel, began to rage at Skirrel through the netting. Skirrel paid no attention to his baffled enemy, although under ordinary circumstances he would have come to the netting and made a hostile demonstration, these two animals being enemies. Timmy continued to rage at Skirrel until the latter had ceased copulation and had assumed a semi-recumbent position on the shelf. Then Timmy went about a foot from the netting and assumed the female position for copulation, smacking his lips as if to invite copulation with Skirrel—Grace had descended to the floor in quest of food. As soon as Skirrel approached the netting Timmy whirled and thrust his forefinger through the netting into Skirrel's eye.

Situation 4. Male taken from his mate and given to a female in an adjacent cage, the first female being left alone.

Observation 7. 10-Timmy-M-c and 11-Grace-Papio— had occupied a cage together for a week, and 7-Becky-M-r occupied an adjacent cage. (All subjects sexually mature.) Timmy was taken from Grace and given to Becky. Timmy copulated with his new mate on the shelf. Grace, now alone and on her shelf, barked angrily and tried to get at Becky through the netting. Timmy was tolled to the floor, leaving Becky and Grace on their shelves, and separated only by the netting. Grace tried to engage Becky in a combat through the netting, but Becky withdrew to the opposite end of the shelf. Then Grace began to smack her lips, and assumed the sexual position, although the male was not in sight. Becky approached the netting, whereupon Grace whirled (she had thrust her hind quarters against the netting) and poked at Becky's face through the netting.

Situation 5. Female at large with band containing dominant male and a sexually mature smaller male. Female detected by dominant male while she is copulating with the smaller male.

Observation 8. 11-Grace-Papio—, 16-Sobke-M-r and 14-Jimmy II-M-c (all three animals sexually mature) were at large with a band containing eight other monkeys. Sobke dominated the band, and Jimmy II had not yet learned to dominate Grace. Sobke and Grace frequently copulated, but at times Grace tolled Jimmy II to a place secluded from Sobke and invited him to copulation. The male baboon's sexual organ being much larger than the male macaque's and of different formation, Grace's sexual hunger seems to be insatiable when she is denied access to the male baboon.

Sobke was perched in a tree outside the yard, and Grace and Jimmy were in the yard, where I was seated making observations. The latter two animals were chattering at me, soliciting food, when Grace began to smack her lips and assumed the sexual position in invitation to Jimmy II. He mounted her, and copulation was well in progress when Grace and I heard a noise in the tree above us. We saw Sobke approaching, croaking angrily and evidently bent on an attack. Grace gave her hind quarters a quick jerk, dismounting Jimmy II. She then began to bark angrily and dashed at Jimmy II, who fled up the side of the cage to escape her attack. Sobke joined in the chase. When Jimmy II made good his escape Grace invited Sobke to copulation, thus terminating the episode.

Observation 9. 1-Bridget-M-r, 4-Pat-M-r, and 2-Mike-M— (sexually mature but not full grown) had been at large several months. Pat was the dominant male and Bridget dominated Mike. During Pat's absence in a neighboring tree Bridget invited Mike to copulation. Pat descended upon them before the act was completed, and Bridget dismounted Mike with a great show of anger and led Pat in pursuit of Mike. This and the above episode may be regarded as characteristic of any monkey when in danger of an attack by a larger one. I have often made such observations as the following one: Two small monkeys were eating in close and peaceful proximity to one another. A larger monkey approached with threatening croaks, obviously intent on an attack. The monkey nearest the approaching enemy quickly turned upon his small companion, and by screaming at him angrily enticed the large monkey to join him in pursuit of his innocent victim. Such behavior is of daily occurrence among monkeys when they are at large.

Situation 6. Female and five males having access to the alley and four cages. One of the males is sexually mature, one is sexually immature and three are eunuchs. A male baboon, many times larger than any of these animals, is given access to them.

Observation 10. 11-Grace-Papio— (sexually mature), 14-Jimmy-II-M-c (sexually mature), 24-Mutt-M-cr (sexually immature) and the three eunuchs (one adult size and two smaller than adult size) had had access to the alley and four of the cages for a week. 12-Sandy-Papio— (sexually mature and of great size as compared with the other five monkeys) was then allowed to enter the alley.

Before Sandy's admission to the band Jimmy II, who had previously allowed Grace to dominate him, dominated the female and the four males. Grace copulated freely with him, but whenever she encountered any of the smaller monkeys in the alley during one of Jimmy II's frequent absences in one of the cages, she would copulate with them. I had frequently observed her surrounded by Mutt and the three eunuchs, copulating with one after another. The eunuchs were more apt to indulge in homosexual copulation than in copulation with the female, but they were not infrequently observed cohabiting, rather perfunctorily, with the female.

For several days after Sandy's admission to the band the three eunuchs screamed with rage whenever he copulated with Grace. Jimmy and Mutt made no demonstration whatsoever on these occasions. The eunuchs' behavior is all the more remarkable in that, although they are ordinarily very timid, and especially afraid of Sandy, they would pull his fur when they found him copulating with Grace.

Situation 7. Several males and females at large. Number of each sex sufficient to enable each animal to have frequent natural sexual relation.

Observation 11. 16-Sobke-M-r (sexually mature), Jimmy II-M-c (sexually mature), 24-Mutt-M-cr (sexually immature), 22-Daddy-M-c (adult eunuch), 20-Chatters-M-c (immature eunuch), 18-Baby-M-c (immature eunuch) and the following sexually mature females had been at large for several weeks: 11-Grace-Papio—, 3-Kate-M-r, 7-Becky-M-r, 5-Maud-M-r and 9-Gertie-M-cr. They wandered freely about the laboratory yard, through the trees and over the tops of the laboratory and the cage. During this time I was able to make a large number of observations, which will be summarized here, rather than given separately and in detail. I found that, although Sobke dominated the band, and could therefore have as frequent sexual relations with any of the females as he desired, he, like all the other males, indulged in homosexual relations. His case is especially interesting, since he was acquired when quite small, and has spent much of his time at large, in company with both males and females. I cannot recall any time when he was confined without at least one female companion. Nevertheless, during the time now under discussion he would approach a smaller male, smack his lips and mount the object of his homosexual desires with evidence of considerable sexual excitement. He copulated with the females more frequently than with the males, and his homosexual behavior was of decidedly less frequent occurrence several months after he arrived at sexual maturity than it was during his sexual immaturity. The same kind of observations were made with reference to Jimmy II: even after he became sexually mature, and had free, outdoor access to females, he would use male monkeys as he used females, but this behavior became much less frequent after sexual maturity than it was during sexual immaturity.

The eunuchs and the immature male (Mutt) were apt to detach themselves from the other members of the band, and to engage in such activities as mock fights, flea-hunts, races through the trees, etc. After a period of play they would huddle together, with arms around one another. Much smacking of lips would follow, and then they would copulate with one another, first one animal, then another, assuming the female position.

During the time that these eleven monkeys were at large I was never able to observe a sexually mature (uncastrated) Monkey assume the female position for copulation with a weaker fellow. Sobke, for example, would use Jimmy II as he would use a female, but would not assume the female position for Jimmy II. On the other hand, even the adult eunuch would assume the female position for Mutt and Baby, both of whom were much smaller and weaker than he. Sobke was always larger than Jimmy II, but before these two animals arrived at sexual maturity one was as apt to assume the female position during homosexual relations as was the other.

The only instance of homosexual relations between females that I could attribute to sexual desire on the part of both animals occurred when I allowed Kate to join the band. She had not had access to her daughter, Gertie, for more than a year, but as soon as she and Gertie met outdoors they rushed into an embrace, following which Gertie assumed the female position and Kate mounted her daughter. The mother made male copulative movements, and both animals smacked their lips and displayed marked excitement. This behavior was never repeated, although the two animals were at large together for several weeks.

Situation 8. Mature male and immature male, having formed a friendship for one another, are separated.

Observation 12. 14-Jimmy II-M-c (sexually mature) and 24-Mutt-M-cr (sexually immature) had been with a band consisting of females and other males. They all had access to the alley and four of the cages. Although Jimmy II cohabited with the females and the eunuchs, he and Mutt were usually seen perched upon a shelf together. Flea-hunting and affectionate embraces usually terminated in homosexual relations, Mutt always assuming the female position. After they had been together two weeks Jimmy II was removed from the band and placed in a cage with 7-Becky-M-r for one week. During this week of confinement with Becky, Jimmy II copulated with her freely. At the end of the week he was allowed to rejoin the band. As soon as he and Mutt caught sight of one another they rushed into an embrace, smacking their lips and making crooning sounds. Both animals quickly manifested marked sexual excitment, and when Jimmy mounted Mutt the latter even rotated his head to bring his lips in contact with those of his friend. I have found that friendships between immature males and mature males are of frequent occurrence, and that they seem to have a sexual basis.

Situation 9. Male, occupying cage with female, is supplied with a nonprimate companion, the female not being removed.

Observation 13. 6-Jocko-M-c and 3-Kate-M-r, both sexually mature, occupied the same cage. A 4-foot gopher snake was thrown into their cage. Kate took refuge on her shelf, but Jocko cautiously approached the snake, lying stunned and almost motionless upon the floor. Jocko finally mustered sufficient courage to lift the snake's tail from the floor and inspect its anal orifice. He then bestrode the snake, seized its body in his two hands, and endeavored to copulate with it. When the snake began to squirm the monkey shrieked and fled to the top of the cage. But he made repeated attempts to approach the snake, which drove him away each time by blowing and thrusting out its tongue.

Observation 14. Jocko, still occupying a cage with Kate, was supplied with a kitten, a puppy and a fox in succession. He attempted sexual relations with each of them after he had inspected their genitalia.

Observation 15. A fox was given to a band of monkeys, including females and sexually mature 16-Sobke-M-r and 14-Jimmy II-M-c. Both males made frequent inspection of the fox's genitalia (the fox was a male) and attempted to copulate with it. 10-Timmy-M-c manifested similar behavior when the fox was given to him, but he finally killed it.

Situation 10. Females at large in a band containing males are given access to a male dog.

Observation 16. 5-Maud-M-r and 3-Kate-M-r, both sexually mature, were at large with a band containing males. A small mongrel dog visited the yard now and then. On his approach all of the monkeys would take to the trees and chatter threateningly. But Maud finally descended to the ground and assumed the female position for copulation. The dog mounted her, dog-fashion, and partially entered her. She displayed marked sexual excitement, and ever thereafter would descend to the ground and copulate with the dog whenever he entered the yard. Kate would descend to the ground and assume the sexual position, but would flee before the dog could embrace her. Maud finally offered herself to a strange dog, and the animal bit off her arm. Since then all of the monkeys have shown hostility to dogs.

Situation 11. Male monkey in contact with human.

Observation 17. 8-Jimmy I-M-c (sexually mature), while at large with a female, discovered a human infant lying in a hammock outdoors. The infant was too young to caress the monkey, but Jimmy I promptly endeavored to copulate with the infant.

Observation 18. 14-Jimmy II-M-r invariably attempts to copulate with my hand whenever I stroke him, in spite of the fact that he has been repeatedly cuffed for it, and has never been encouraged in such behavior.

Situation 12. Mature male, after a week of confinement without companions.

Observation 19. Of all my male monkeys only 6-Jocko-M-r (mature) has been observed to masturbate. After a few days confinement he would masturbate and eat part of his semen. I have reason to believe that he lived under unnatural conditions for many years before I acquired him. In view of this fact that not one of seven sexually mature monkeys masturbated after several weeks of isolation under conditions that favored a fairly healthy mental and physical life (close proximity to other monkeys, large cage, warm climate), I am inclined to believe that masturbation is not of normal occurrence among monkeys.

Situation 13. Mature female, after a week of confinement without a companion.

Observation 20. 3-Kate-M-r, after a week of isolation, smacked her lips and assumed the sexual position whenever the male in the adjacent cage approached. A reported case of masturbation by this animal proved to be mere reflex scratching of the genitalia, which were irritated by partially dried menstrual discharge. Kate would assume the sexual position whenever I approached her cage, and when a ranch hand voided urine in her presence she displayed marked sexual excitement, smacking her lips and croaking invitingly.

Observation 21. 5-Maud-M-r, after a week of isolation behaved in essentially the same manner as did Kate in observation 20.

Situation 14. Male, threatened by larger male and unable to escape.

Observation 22. When 12-Sandy-Papio— (mature) was first admitted to the alley band, of which 24-Mutt-M-cr (immature) was a member, all of the band excepting Grace fled. Sandy, it will be remembered, is a very large baboon, and Mutt is an immature rhesus, hence very tiny in comparison with Sandy. When the band scattered on the approach of the baboon, Mutt darted into a cage and crouched in a corner, on the floor. Sandy followed him, leering at him threateningly. Mutt squealed in terror, and looked about him as if seeking an avenue of escape. Finding none, he assumed the female sexual position, but as Sandy approached, now displaying only friendliness and sexual excitement, the little monkey darted between his legs and escaped.

Observation 23. 28-Scotty-M— occupied a cage adjacent to that occupied by 10-Timmy-M-c. Scotty is sexually mature, but not yet of adult size. He is very timid and Timmy is a savage adult. Timmy forced the netting partition loose and entered Scotty's cage. Scotty fled in terror, shrieking and gnashing his teeth. When Timmy finally caught him and began to bite him Scotty assumed the female sexual position, thereby effecting a temporary escape, since this diverted Timmy sufficiently to enable his victim to dart past him.

Situation 15. Female threatened by larger female and unable to escape.

Observation 24. 11-Grace-Papio— and 9-Gertie-M-cr (both sexually mature) were brought together in the alley. Grace at once attacked Gertie and began to bite her. Gertie assumed the sexual position, and was mounted by the larger female. Grace manifested no sexual excitement, and made no copulatory movements. In a moment she returned to the attack, and Gertie again assumed the sexual position, but this time eluded the baboon and was allowed to escape to another cage.

Observation 25. When 11-Grace-Papio— (mature) was first admitted to an outdoor band of which 3-Kate-M-r (mature) was a member, she was attacked by Kate. For several days Kate was able to pounce upon the baboon's back, bite her and escape. But the baboon finally cornered her, whereupon Kate promptly assumed the sexual position, which did not avert the attack. It is unnecessary to multiply instances of this kind, but it may be said that I have witnessed many episodes where a smaller female endeavored to avert a larger female's attack by assuming the sexual position, but that I have never known either animal to display sexual excitement unless the aggressive female's momentary mounting of her victim could be regarded as due to an erotic impulse. The absence of such signs of sexual excitement as smacking the lips and copulatory movements, and the continued display of hostility on the part of the female while she is mounting the object of her attack render it unlikely that the mere act of mounting under these conditions occurs in response to sex hunger. On the other hand, the tendency of the weaker female to offer herself to the aggressive female for copulation is clearly related to a desire to escape rather than to sexual desire. The next observation will tend to confirm this opinion.

Situation 16. Female in a condition to render copulation inacceptable made accessible to a male.

Observation 26. A week after the birth of a full-term infant, which was dead when first discovered, 9-Gertie-M-cr was made accessible to 16-Sobke-M-r (both animals sexually mature). Before the birth of her infant Gertie had always been on good terms with Sobke, and had never displayed fear in his presence. But when he approached her on this occasion, smacking his lips and eager for copulation, she gnashed her teeth and squealed in fear. The male pursued her, and when she was cornered, Gertie assumed the sexual position. When Sobke reared upon his hind legs Gertie darted past him. This episode was repeated several times, the female always effecting her escape before the male could copulate, and at no time displaying sexual excitement. A week later she submitted to copulation with Sobke, and displayed sexual excitement.

Observation 27. 3-Kate-M-r (mature) was severely bitten by a dog while she was at large. Her tail was almost completely denuded of skin and fur, and her body was lacerated in places. She was put in a cage by herself for a week, then made accessible to 10-Timmy-M-c (mature). She was still weak and inclined to mope. Like Gertie in observation 26, she fled from the male, and assumed the sexual position only when she was cornered. The animals were separated as soon as it was apparent that her assumption of the sexual position was a purely defensive measure.

Situation 17. Young sexually mature male attacked by sexually-mature female.

Observation 28. 11-Grace-Papio— (mature) was admitted to the cage occupied by 28-Scotty M—. Scotty was sexually mature in the sense of being able to discharge the full sexual function, but had not yet attained adult size, and was very timid. Grace advanced toward him, barking and threatening an attack. When she began to bite him he assumed the female sexual position, whereupon Grace mounted him, smacking her lips. She made no copulatory movements, and at once dismounted and assumed the female position. The male then copulated with her.

Situation 18. Infant monkey in danger of attack.

Observation 29. 13-Tiny-M-cr (age 5½ months) was momentarily abandoned by her mother (7-Becky-M-r) while the latter sat upon the sleeping box roof and fought the members of the alley band through the wire netting that separated them. Tiny was whimpering and running back and forth when 11-Grace-Papio— dashed at her, barked, and clawed at the netting. Tiny's assumption of the sexual position had the appearance of a pure reflex, so quick was it, and so quickly followed by a retreat to her mother's arms.

Observation 30. 24-Mutt-M-cr, when 6 months old, was observed to assume the female sexual position while his mother was absent from the shelf. He was whimpering and running back and forth on the shelf, when 10-Timmy-M-c (mature) threatened him from the other side of the netting. The infant assumed the female sexual position momentarily, then fled down the side of the cage to his mother. This kind of behavior may have been manifested earlier.

IV. CLASSIFICATION OF SEXUAL REACTIONS AS EXPRESSIONS OF REACTIVE TENDENCIES

1. *Tendencies to Seek Sexual Satisfaction.*

A. *Male Tendencies*

(a) Tendency to engage in typical sexual intercourse with females.

(b) Tendency to increase sexual excitement by preliminary examination of the female's genitalia, or by chasing and biting the female.

(c) Tendency to use a younger or weaker male as a female.

(d) Tendency to play the rôle of female to a copulating male.

(e) Tendency to attempt copulation with non-primates and humans.

(f) Tendency to masturbate (probably developed only under abnormal conditions).

B. *Female Tendencies*

(a) Tendency to engage in typical sexual intercourse with males.

(b) Tendency to play the rôle of male to younger or weaker female.

(c) Tendency to play the rôle of female to friendly female.

(d) Tendency to solicit copulation with non-primates.

2. *Tendencies to Assume the Female Sexual Position as a Defensive Measure.*

A. *Male Tendencies*

(a) Tendency to assume the female sexual position when attacked by a more powerful fellow of either sex.

B. *Female Tendencies*

(a) Tendency to assume the female sexual position when attacked by a more powerful fellow of either sex.

3. *Tendencies to Seek to Lure an Enemy to Attack by Assuming the Female Sexual Position.*

A. *Male Tendencies*

(a) Tendency to lure a male enemy to attack by assuming the female sexual position.

B. *Female Tendencies*

(a) Tendency to lure a female enemy to attack by assuming the female sexual position.

My analysis of the material from which the thirty observations recorded in the preceding pages were taken, at first inclined me toward a classification in which there would appear only the three general tendencies that appear in the above table, viz.: (1) A tendency to seek sexual satisfaction, (2) A tendency to assume the female sexual position as a defensive measure, (3) A tendency to lure enemies to attack by assuming the female sexual position. Had this scheme of classification been adopted, lists of the typical expressions of each of these three tendencies would have been given instead of the lists of specific tendencies that appear in the table. But the viewpoint from which I have come to regard animal and human behavior, taken inclusively, as material for a separate branch of natural science which may be made to serve as an important foundation for various applied sciences finally induced me to adopt the method of classification that appears above. According to my view, the behavior of an organism is the expression of reactive tendencies which have specific representation in its structure. Some of these tendencies have an *inherent* structural representation, such as, e.g., the tendency that finds expression in the kitten's spit and slap when it first encounters the dog-odor—behavior which may be observed in a kitten before its eyes are opened, and which cannot be attributed to the modifying effects of any previous experiences. Other tendencies owe their existence to two factors, viz.: (1) An inherent capacity for post-natal structural modifications by experience; these modifications by their appearance, add the tendencies of which they are the appropriate bases to the list of the organism's properties. (2) The operation of environmental influences that help to produce the necessary structural changes. Any habit-reaction may be regarded as the expression of an acquired tendency of this kind.

My conception of behavior as reducible to expressions of specific reactive tendencies might easily lead to an endless multiplication of such tendencies to account for the apparently innumerable separate modes of organic activity—especially in view of the possibilities afforded by the extreme plasticity of the nervous system—if it did not include something more than the above generalizations. Lasurski (2), whose *Hauptneigungen* bear many points of resemblance to the reactive tendencies of my conception, avoids this danger by stopping short at the point at which he recognizes various relatively separate directions in which a given individual's activities may go in response to a limited number of principal inclinations. He regards these inclinations (tendencies) as artificial abstractions to which, nevertheless, human personality is most profitably and conveniently reducible. McDougall (3) calls attention to the fact that " The activities of each species are directed almost exclusively towards a small number of special ends—reproduction, the securing of food, the escape from danger, the protection of the young, the violent destruction of whatever opposes these great tendencies, and a few others that differ from species to species." To this he adds: " The concentration of the animal upon any of these ends does not depend upon its acquired experience, but upon some feature of its innate constitution; and that feature is what we commonly and properly call an *instinct*, an innate tendency to strive after some end of a particular kind, an *innate conative tendency*."

The reactive tendency of my definition differs from Lasurski's *Hauptneigung* in that it is meant to connote something more than an artificial abstraction, and to refer to specific properties of the organism rather than to the generally inclusive traits of personality that Lasurski has in mind. It differs from McDougall's *innate conative tendency* in its recognition of the fact that the features of an animal's innate constitution are plastic, and capable of modification by experience. I am also inclined to approach the analysis of behavior from a somewhat different viewpoint than that which is implied in McDougall's statements. In dealing with behavior one is apt to be diverted from the most proximate aspect of the phenomena under consideration by estimating the facts solely with reference to the ultimate needs of the individual or, more usually, of the species. It is somewhat artificial, I believe, to assume that a given sequence of activities is set in operation by outer stimuli acting in conjunction with a need which is more apt to be a product of the biologist's analysis than (in other than a rather mystical sense) dynamically a part of the animal's reactive equipment. The preferable course is to identify *individual hungers* which are the product of inner, physiological events and environmental stimulations. The satisfaction of a given hunger may or may not be conducive to the welfare of either the individual or the species—may or may not correspond to a biological need. The total phenomenon with which the behaviorist is concerned in a given case consists of a sequence of events of which the first member is usually, but not always, an external situation. Then come the physiological processes that produce the hunger-impulsion to which the reaction is to be ascribed. The identification of a reactive tendency becomes possible whenever we are able to predict that the operation of a given hunger-impulsion will be directly followed by a series of activities which conform to a known type.

The existence and nature of a given hunger is, of course, arrived at by inference; but this does not necessarily call for a departure from a purely objective attitude toward the facts. If, as Watson (4) suggests, the behaviorist may use the term "consciousness" as it is used by other natural scientists, no insuperable difficulty ought to be encountered in the construction of criteria for the identification of a hunger as a relatively independent dynamic unit. Such criteria would take into account the facts concerning the physiology of the sense-organs to which we already have access; and would recognize the various possibilities for experiencing specifically different satisfactions by employing different modes of stimulating the sense-organs. For example, when I entered the laboratory yard this morning carrying a pail of loquats, the coyote leaned against the large meshes of the wire fence that confines him and whined until I scratched his head; the monkeys gave their characteristic food-calls until I gave them loquats; and after the male monkeys had eaten this agreeable addition to their breakfast they sought the females and copulated with them. I did not need to raise a question as to the contents of each animal's state of consciousness to assist me in the identification of the coyote's dog-like hunger for a mild irritation to his cutaneous sense-organs, or the monkeys' hunger for the various stimulations that are derived from eating food, etc. The coyote may or may not have had a mental picture of the head-scratching or the monkeys of the loquats that usually appear these days whenever I put my hand into the little tin pail; but I am quite sure that these animals were clamoring in response to the particular hungers that I have come to recognize, and that their behavior, the types of which I could have predicted before I entered the yard, was the expression of definite organic properties.

The essential points of the above discussion are these: (1) The essential factors concerned in behavior phenomena are (a) the action of physiological processes usually operating in conjunction with environmental forces, in the production of (b) hungers which impel the individual to manifest (c) activities, the particular types or modes of which are to be ascribed to (d) specific organic properties (reactive tendencies). (2) These reactive tendencies are most conveniently classified with reference to the individual hungers that bring them to expression. (3) The term "reactive tendency," according to my definition, is meant to designate something more specific than an inclination to direct activity toward one of a limited number of general ends, and to include both the innate and the acquired features of an individual's reactive mechanism.

CONCLUSIONS

At least two, and possibly three, different kinds of hunger, or needs of individual satisfaction, normally impel the macaque toward the manifestation of sexual behavior, viz., hunger for sexual satisfaction, hunger for escape from danger and, possibly, hunger for access to an enemy.

Homosexual behavior is normally an expression of tendencies which come to expression even when opportunities for heterosexual intercourse are present. Sexually immature male monkeys appear to be normally impelled toward homosexual behavior by sexual hunger. The fact that homosexual tendencies come to less frequent expression in the mature than in the immature male suggests the possibility that in their native habitat these animals may wholly abandon homosexual behavior (except as a defensive measure), on arriving at sexual maturity.

Homosexual behavior is of relatively frequent occurrence in the female when she is threatened by another female, but it is rarely manifested in response to sexual hunger.

Masturbation does not seem to occur under normal conditions.

The macaque of both sexes is apt to display sexual excitement in the presence of friendly or harmless non-primates.

It is possible that the homosexual behavior of young males is of the same biological significance as their mock combats. It is clearly of value as a defensive measure in both sexes. Homosexual alliances between mature and immature males may possess a defensive value for immature males, since it insures the assistance of an adult defender in the event of an attack.

REFERENCES

(1) Freud, Sigmund. Drei Abhandlungen zur Sexualtheorie. Vienna. 1905.

(2) Lasurski, A. Ueber das Studium der Individualität. *Pädagogische Monographien*, XIV Band. Leipzig. 1912.

(3) McDougall, Wm. The Sources and direction of psycho-physical energy 1913. *American Journal of Insanity*, vol. 69, no. 5, p. 865.

(4) Watson, John B. Psychology as the behaviorist views it. *Psychologica* 1913. *Review*, vol. 20, no. 2, pp. 158-178.

VISUAL PATTERN-DISCRIMINATION IN THE VERTEBRATES—I

PROBLEMS AND METHODS

H. M. JOHNSON

From the Nela Research Laboratory,
National Lamp Works of General Electric Company

GENERAL BEARING OF THE PRESENT INVESTIGATION

The present work grew out of an interest in the question of the comparative ability of different vertebrates to discriminate detail in visual objects. The theory of sexual selection, which is of considerable historical importance at least, assumes that certain animals discriminate intricate markings of plumage or of hair. The theory of natural selection also assumes that some animals can discriminate details in visual objects, although its demands are less severe and less definite than are those of the theory of sexual selection. The question is of interest to some students of behavior apart from its direct bearing on either theory.

As regards the factor of vision in the theory of sexual selection, it is evident that two distinct questions are involved. One is, Do animals react to differences in marking ? Are individuals possessing a coat of a given pattern aided or hindered thereby in securing a mate ? This question may be attacked without studying the vision of the animals. If one were to observe the courting behavior of a large number of individuals and note the number and conditions of copulation or mating of all the members of the group, correlation of these data with the kind of markings possessed by the individuals would throw light on the question. The other question is, Can the animal respond to differences in visual detail, and if so, how great must these differences be ?

CHOICE OF RESPONSES FOR STUDY

The observable facts in a study of an animal's special senses are the responses which the animal makes to stimuli affecting the sense organ. If the study is regarded as one in behavior, these data are considered as " explained " when they are satisfactorily referred to the characters of the stimuli and the structure, condition and physiological processes of the organism. If the study is to be stretched into one of (hypothetical) " mental content," which some consider the subject-matter of " animal psychology," it is necessary for the student to make certain arbitrary assumptions regarding the animal's possession of " mental states " and regarding the degree of similarity obtaining between these hypothetical mental states and his own. Postulating the validity of these assumptions, and basing his inferences on them as much as on the observed facts, the student may now attempt to " translate " the animal's behavior into " terms of his own conscious experiences." This sort of treatment of the data has been severely criticized on the ground of unwarrantability. The criticisms have not been altogether effective, however. But it would seem advisable in any event for students to report all the stimulus-conditions and all the facts of behavior before indulging in interpretations in terms of mental content, in order that questions of fact and questions of interpretation may not become confused by the readers. Whatever one's standard of interpretation may be, the animal's responses remain the same.

The responses chosen for study may of course be either muscular or glandular. Pavloff and members of his school have devised the well-known method of studying the effect of sensory stimuli on the saliva-reflex. Yerkes and Morgulis[1] have discussed certain shortcomings in the technique. Some of these the experimenters themselves had considered. Could the number of variables be reduced, a very interesting and valuable set of data are possible. The reason why some experimenters have chosen muscular responses is merely a greater interest in them. It should be remarked also that we are not yet warranted in predicting the effectiveness of stimuli in occasioning muscular responses, from their effectiveness in occasioning glandular responses. A stimulus-value or stimulus-difference sufficient to produce a change in the rate of saliva-secretion or of the quality of the saliva might be quite inadequate to cause an animal to choose one feeding-place and reject another. Taken at their face value, some of the results in audition of the dog reported by members of Pavloff's school seem to indicate that this is actually true.

---

[1] Yerkes, R. M., and Morgulis, S.: The Method of Pavloff in Comparative Psychology. *Psychological Bulletin*, 1909, pp. 257 ff.

In the present study it seemed advisable at the outset to set some problems of a different type from those heretofore attacked, and to develop methods of studying those problems. This arose from consideration of certain limitations of apparatus used in the standard methods of studying vision in animals, and of certain limitations of the current problems themselves.

STANDARD METHODS OF STUDYING VISION

For some years vision in animals was investigated by more or less impromptu methods of great diversity. The data thus obtained were at best incomparable. The conclusions drawn from them were often vitiated by the lack of control of physical factors.

In response to a widespread demand for improvement and standardization, Yerkes and Watson[2] published in 1911 the results of an extensive investigation of apparatus and procedure. For studying color-vision they recommended an apparatus consisting essentially of a high-intensity spectrometer system, equipped with devices for selecting monochromatic bands and presenting them to the animal. The stimuli thus obtained are accurately measurable and highly controllable as to wave-length, intensity and saturation. The apparatus meets all physical requirements. Since it has yielded quite definite behavior results, both positive and negative, it seems well established as the standard. No other adequate method has been described up to the present time.

To prepare stimuli for testing the sensitivity of animals to differences in brightness, size and form of visual objects, the authors recommended the use of standard forms presenting a constant difference only in the physical characteristic whose effect is under study. They report that "differences of the compared stimuli as to . . . color . . . texture, position, odor," etc., can be eliminated in their method. The animal to be tested is stimulated by light transmitted through two opal glass screens whose respective illumination is independently controllable. They are covered with mutually interchangeable brass plates in which windows of the desired size and form have been accurately cut and beveled. The windows may conform to any plane figure. Circles, squares, triangles and hexagons are most commonly used.

---

[2] Yerkes, R. M. and Watson, John B.: Methods of Studying Vision in Animals. No. 2, *Behavior Monographs*, Cambridge, Holt, 1911.

Tests of brightness-sensitivity are made with forms geometrically equal but differently illuminated. The apparatus is adequate for this purpose within the limitation of the problem itself. This limitation will be remarked below (page 327).

In testing size-discrimination two circles of different diameter may be employed. The circle used as a standard is usually 6 cm. in diameter, the diameter of the comparison-circle varying between 3 cm. and 9 cm. For form-discrimination the stimulus windows may be a circle 5 cm. or 6 cm. in diameter, used as the standard; the comparison-form being the circle's equivalent, inscriptible or circumscriptible square, triangle or hexagon. As applied to the study of size- and form-discrimination, certain limitations of the method should be noted.

In the study of size-discrimination, two constant stimulus-characteristics other than size must be controlled. These are the *luminous intensity* of the respective forms, and their respective *brightness*. Since these two terms are somewhat variously used in physiological and psychological literature, and since in this paper they have a restricted meaning, I beg the reader's indulgence while the present meaning of the terms is being specified.

In the accepted photometric nomenclature, if the light coming from a source produces on a surface the same illumination as that produced by a standard source at the same distance, both sources are said to have the same *luminous intensity* in the directions respectively given. The standard measure of luminous intensity in America is the *candle*. The *brightness* of a source is taken as the luminous intensity divided by the area of the source; it is usually measured in terms of *candles per square meter* or derivatives thereof.

The opal glass screens limited by the windows therefore serve (1) as sources, each having a certain candle-power; and (2) as visual objects, each having a certain brightness and area. Both screens being equally illuminated and the transmission and diffusion coefficients of the one being respectively equal to those of the other, the *brightness* of the larger and the smaller surfaces would be equal: but their *luminous intensity*, or candle-power, would vary directly as the area exposed. If the *luminous intensity* of the two screens were made equal, the *brightness* of each screen would be inversely as its area.

Suppose the two screens are covered by plates each containing a window, the one 3 cm., the other 6 cm. in diameter. If the two screens are equal in *brightness*, and if a complete image of the larger be formed on the retina, it is evident, *ceteris paribus*, that the animal will be stimulated by four times as much light from the larger as from the smaller form. Thus it is possible for the animal to acquire discrimination on the basis of difference in quantity of luminous flux entering the eye, independently of the difference of extensity of the stimulated parts of the retina. Lashley[3] reports that his white rats began to react to the difference of illumination of the respective alleys of the Yerkes box. To swamp this difference he introduced an additional lamp directly above the Yerkes box. This served the purpose, apparently, by adding enough illumination (an equal amount to each alley) to reduce the proportional brightness-difference to a point below the threshold. It is evident that such procedure does not neutralize the difference of luminous intensity of the respective screens. If an equal brightness be added to each screen by the additional lamp, or if the screens are protected from it, their respective luminous intensities would be directly as their respective areas. It is not clear that this was Lashley's intention. Bingham[4], however, in his work on the chick, assumed this precaution to be sufficient. The fact is masked to some extent by his use of the word " intensities " (op. cit. p. 76) synonymously with " brightnesses " in the present discussion. His birds discriminated a circle 6 cm. in diameter from one 4.4+ cm. in diameter. Bingham reports no control tests to show that discrimination was on the basis of size, rather than of luminous intensity of the stimuli. If he made no control tests his conclusion is of course unwarranted.

If the *luminous intensity* of the respective screens be equalized by reducing the illumination of the larger, or increasing that of the smaller, a difference in *brightness* is ipso facto established. This difference also may serve as a basis of discrimination independently of difference in size.

---

[3] Lashley, K. S.: Visual Discrimination of Size and Form in the Albino Rat. *Journal of Animal Behavior*, 1912, pp. 310 ff.

[4] Bingham, H. C.: Size and Form Perception in Gallus Domesticus. *Ibid*, 1913, pp. 65 ff.

It must be explicitly granted that discrimination based on these characteristics can be detected as such in control tests, so that no one need be deceived in drawing conclusions. My point is merely that control of these factors, at some stage of experimentation, is necessary to warrant conclusions; that both factors cannot be controlled simultaneously; and that the method of control sometimes proves troublesome. Breed[5] obtained positive results with a chick, keeping these factors variable throughout experimentation. Other students have been less successful. Yerkes[6] recently recommended a different course: that one present stimuli differing in more than one characteristic—e.g., in brightness and form as well as in size, until discrimination on *some* basis appears. This course simplifies the problem at the beginning of training. Certainly some advantages are thus to be gained. Perhaps the greatest drawback is the risk of a large waste of time. It has happened that an experimenter discovers after several weeks of training that the animal had learned to react to difference of e.g. brightness, and had not been affected by the other stimulus-differences. It would seem that a difference in luminous intensity is especially objectionable since in dark surroundings the animal can choose the brighter or darker alley without attending specifically to the stimulus-forms.

With the apparatus under discussion some experimenters cause the animal to be fed near the positive form, or to pass quite near it, at least, after each correct choice. Thus it is possible for olfaction to become a factor. Lashley (op. cit. supra) reports disturbance of this kind in his work on the rat, at a stage when discrimination was not present. Substitution of a new stimulus-plate for one which has been used for some time may introduce a disturbance which might be unjustly ascribed to the animal's inability to discriminate visually. It is difficult to exclude olfaction, although its presence may be detected in control tests.

The foregoing remarks apply only to questions of convenience in using the standard apparatus. It possesses also a fundamental defect which impresses the writer as serious. An apparatus for quantitative study should permit of change by insensible gradations from a given stimulus-value to any other stimulus-value desired, within the limits of the instrument. The standard apparatus permits such changes in the case of size-differences, it being necessary only to prepare a sufficiently large number of plates. This is not possible in the case of form-difference. Suppose an animal learns to discriminate between a circle and triangle, and maintains a perfect habit throughout a satisfactory set of changes of size, of illumination, and even of surroundings of the test-objects. We may safely conclude that he is reacting to the constant difference of form of the test-fields. But we cannot say, in terms of stimulus-factors, how much of this form-difference is necessary to effect discrimination. It is indeed possible to prepare a series of plates changing by imperceptible degrees from the plane triangle through regular trilateral figures (such as certain plane projections of spherical triangles) to the circle; keeping the figures equivalent throughout the series. No experimenter has yet attempted this plan. It involves considerable expense and mechanical skill, and may for this reason be impracticable. Meanwhile we are without an apparatus for the study of form-discrimination which meets the fundamental requirements of a quantitative study.

---

[5] Breed, F. S., " Development of Certain Instincts and Habits in Chicks," *Behavior Monographs*, vol. I, No. 1.
————, " Reactions of Chicks to Optical Stimuli," *Journal of Animal Behavior*, 1912, pp. 280 ff.

[6] Yerkes, R. M., "The discrimination method." This Journal, vol. 2, 1912, pp. 142 ff.

To consider now a limitation of the problem of form-discrimination itself: it is questionable whether the data obtainable in this study are indicative of an animal's ability to react to differences of visual detail. Perhaps a definite opinion is not warranted by the evidence now at hand. But the circular and square windows, for example, of the Yerkes-Watson apparatus merely limit the perimeters of two light sources of equal brightness and extent. If natural conditions never require an animal closely to scrutinize the borders of objects so nearly alike in all other respects, he may acquire such specialized discrimination with great difficulty or not at all. Supplementary data are necessary to justify one in referring the learning records to the character of the animal's visual equipment, to the character of his "attention" or to the limits of his ability to learn. It impressed the writer some time ago that an improvement of the method used by Casteel and the development of the problems suggested by his work should throw light on the question at issue.

CASTEEL'S EXPERIMENTS IN PATTERN-DISCRIMINATION

Casteel[7] worked on the painted turtle, using a modified form of the Yerkes box. The animals were trained to choose between two food-boxes, equally illuminated. The food-boxes were " identical in every respect," except that each carried a different pattern, painted directly on the box or on cardboard covering the box. The patterns consisted of alternate " black and white " stripes respectively equal in width. The experimenter set two problems: discrimination between a system of horizontal striae and one of vertical striae; and between two systems of striae of different widths but lying in the same direction. With respect to the former, it may be remarked that Casteel did not ascertain how small a system could be distinguished as a striate field: i.e., what band-width was just distinguishable at a given distance from a field of equal mean brightness uniformly disposed. This would have added greatly to the value of an already interesting set of results. In both experiments Casteel obtained discrimination from several animals in less than 600 trials. It is unnecessary to point out the difficulty of adapting Casteel's method to quantitative work.

ELEMENTARY PROBLEMS IN PATTERN-DISCRIMINATION

Broadly the term pattern-discrimination may be used to designate discrimination between visual fields equal in outline, area and average brightness, differing only in the respective disposition of their brightnesses. The present work is an attempt to study four elementary problems included in such a study.

1. The stimulus-threshold for striation. Given two striate fields, the striae on one of which are too small to be resolved by the eye at the given distance, the striae on the other field being large enough to be distinguishable: How great must be the width of the individual striae on the second field to occasion discrimination between it and the sensibly uniform field ? The visual angle subtended by one of the striae may be taken as a convenient measure of the animal's *visual acuity* under the experimental conditions.

2. The difference-threshold for size (and conversely for number) of visible striae. Given two systems of striae, the width of the members of one system being greater and their number

---

[7] Casteel, D. B., " Discriminative Ability of the Painted Turtle." *Journal of Animal Behavior*, I, 1911, pp. 1 ff.

correspondingly fewer, than those of the members of the other system: How great must this difference be in order to effect discrimination ? To what extent does the difference-threshold depend on the absolute size of the members of the two systems ?

3. The difference-threshold for direction of visible striae. Given two systems of striae the members of the two systems being respectively equal in width but lying in different directions: How great a difference of direction is necessary to effect discrimination ? To what extent does the difference-threshold for direction depend on the absolute width of the members of the two systems ?

4. The threshold for contrast. Given two systems of visible striae, the members of which are respectively equal in width and direction, the juxtaposed striae on one field being of equal brightness, and those on the other field being of unequal brightness: How great must the brightness difference on the second field be in order to effect discrimination between it and the sensibly uniform field ?

The fourth problem might be called that of brightness-discrimination. This term is now used in behavior literature, however, to designate a particular form of brightness-discrimination in animals, which is studied by the Yerkes-Watson method. The two problems are of course quite different. In the Yerkes-Watson problem, the two screens, having the same area and differing in brightness, differ also in luminous intensity; each field is of sensibly uniform brightness; and the "contrast-areas" are widely separated. The present problem is one of discrimination between two fields of equal luminous intensity, one of which has a uniform surface brightness, while the other presents a system of alternate bright and dark bands in juxtaposition. The degree of contrast between the juxtaposed bands on the one field requisite to discrimination being the factor sought for, it is evident that the results obtained by this method are not necessarily comparable with those obtained by the Yerkes-Watson method. I therefore prefer to treat this problem as one in pattern-discrimination.

A large number of changes may be rung on the four problems suggested above. The results would depend on the range of wave-lengths used, the luminous intensities of the fields, the brightness of the surroundings, etc. Further combination of two or more stimulus differences might be found to have an interesting effect on the threshold. For example, if two systems of striae were made to differ in width of their respective members, as well in direction, the difference-threshold for direction might be lowered even though the width-difference were subliminal when the two systems lay in the same direction. In the present work I have limited the attack to the four elementary problems, under one set of experimental conditions. The results are presented as holding good only under those conditions. But it impresses the writer that a successful method having been satisfactorily developed, a rich field is open for further extension.

METHOD OF PREPARING AND PRESENTING THE STIMULI

For investigating the first three problems a single instrument has been used for preparing the test-fields, with very satisfactory results. Since it has not been used before in animal experimentation, and since familiarity with its principles is necessary to adapt it to such work, it requires detailed description. It consists essentially of two systems of fine opaque lines ruled on glass, the width of the lines and of the clear interspaces being equal. When these two systems are rotated over each other about an axis perpendicular to the surfaces of the glass, a series of bright and dark bands of equal width appear. The size and number of these striae are reciprocal, dependent on the angle of rotation, and are highly controllable. The direction of the striae is variable at will. The instrument possesses certain peculiar features which are especially advantageous in this work. The luminous intensity does not change under experimental conditions. The mean brightness of the field remains constant provided the area selected include an equal number of dark and bright bands of the same length, or if it be large with respect to the area of a given band. Possible disturbances from constant differences in olfactory stimuli are absolutely neutralized in all stages of experimentation. Change from any stimulus-value to any other can be made by insensible gradations. Large differences in pattern can be made without changing any other stimulus-factor In addition to these peculiar features, the apparatus is not unduly expensive; it permits an instantaneous and practically noiseless interchange of stimuli to be made from the operator's chair; and its operation is quite simple.

The instrument reached its present form by a number of accretions. In 1906 Behn[8] called attention to certain properties

Fig 1

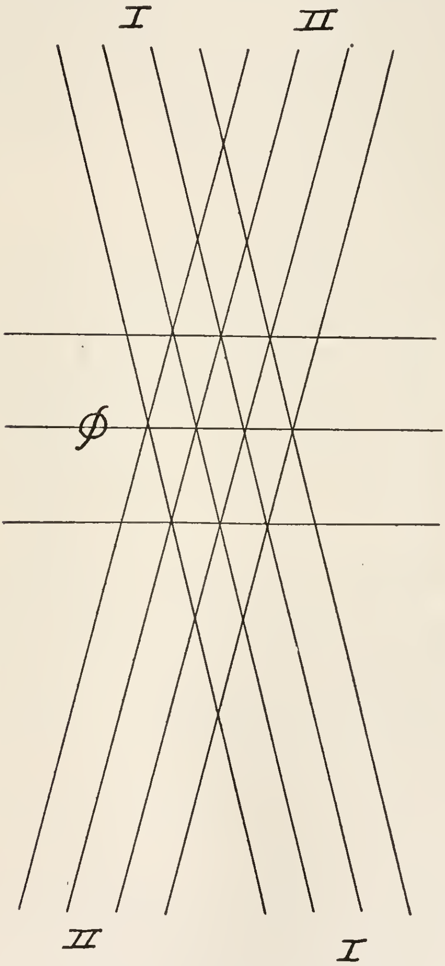
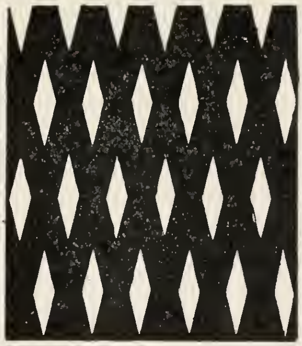


Fig. 2



FIGS. 1 and 2; showing principle of crossed gratings (after Behn).

of superposed gratings. He says: "The points of intersection of two systems (I and II, Fig. 1) of parallel equidistant straight lines always lie in parallel equidistant straight lines (III). If the separation of the lines in systems I and II be equal, the lines III bisect the angle I, II (ϕ). If one substitute for the lines I and II dark bands of perceptible width (Fig. 2), the lines III become bands of maximal brightness; between two such bands lies one of maximal darkness. These striae are easily perceived. . . . . If the angle ϕ between I and II be changed, the separation (l) of the striae III is changed accordingly. If ϕ be small the change in separation is very great, as appears in the relation

---

[8] Behn, U, "Ueber eine neue Dilatometer Prinzip für Projection," *Berichte d. Deutschen Physikalischen Gesellschaft*, IV, 1906, S 207 ff.

$$Sin\frac{\phi}{2}=\frac{c}{2l}$$

. . . . wherein c represents the separation of the lines in I and II. This fact can be utilized in dilatometric demonstrations; generally in rendering small displacements visible; and especially in measuring thickness." Behn used the instrument for measuring small changes in expansion, deriving the linear change from change in size of the visible striae; the bar under observation being attached so as to move one of the gratings, the other end of the bar being fixed. I include a reproduction of Behn's figures.

Ives,[9] who does not refer to Behn's article, restates the relation between the width of the visible striae and the angle of rotation which the former had expressed. In addition to the properties which Behn enumerates, Ives mentions that the mean brightness remains constant through changes in size of the test-bands. (It may be seen from casual inspection of the photomicrographs shown by Ives and by Cobb in the article cited below, that the clear rhombi whose linear arrangement forms the bright striae compose one-fourth the total area of any symmetrical portion of the field.) Ives proposed that the principle be applied to the construction of a test-object for investigation of visual acuity, since no satisfactory instrument then existed and there was a demand for one. He also set forth certain practical considerations governing the choice of grating-width to be used.[10]

---

[9] Ives, H. E., "A Visual Acuity Test-object," *Electrical World*, lv, 1910, pp. 939 ff.

[10] Ives asserts: " The ideal test-object is one in which the size of the detail is the only variable." " The test-object as constructed fulfils the requirements of an ideal test-object. The distance of the object and the flux of light entering the eye remain constant. Dark bands, whose visibility forms the test of acuity, may be varied in their separation from invisibility to easy visibility." The present writer believes this valuation of the instrument should be qualified. The instrument fails in one

The first set of gratings used for this work were mounted by Cobb.[11] The mounting in the present instrument is essentially that of his; in fact some of his patterns were used in making the present castings. I have made two modifications to adapt the instrument to the present work. One of these is the device which permits an instantaneous shift between two given widths of visible striae; the other is the device which permits instantaneous and measurable change in direction of the striae. The following description and accompanying figures are of the apparatus in its present form.

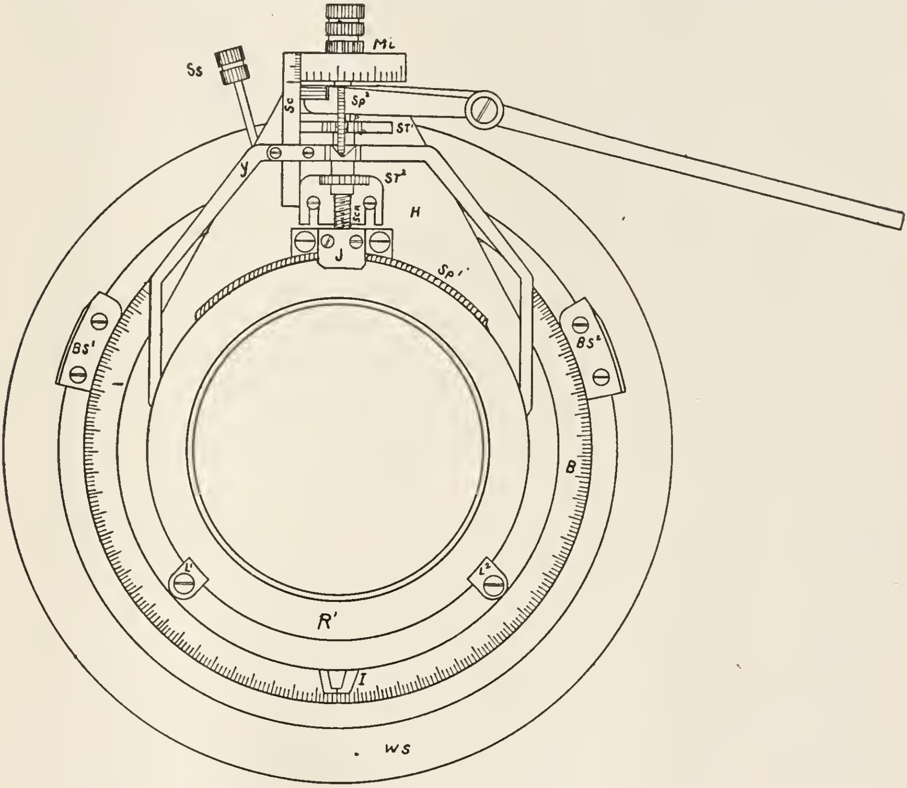


FIG. 3. Mounting for gratings.

---

requirement of an ' ideal ' test-object, which is that the contrast between the dark and bright portions of the field should be sharp. Due to the construction of the bright striae, they appear ' fuzzy ' at all values. For the present work this is not seriously objectionable. For some work it might be.

[11] Cobb, P. W., " The Influence of the Illumination of the Eye on Visual Acuity," *American Journal of Physiology*, 1911, pp. 76 ff.

Each grating is held in a metal ring, R^1, R^2. The two rings bear on each other. Each ring is cut with a shoulder extending from the concave cylindrical surface, to which the grating is cemented. The shoulder is high enough that the two gratings are separated by about 1–64 inch, which is sufficient to prevent their rubbing, but not enough to cause disturbance from parallax at the distance at which the instrument is used. The ruled surfaces of the gratings are placed interior. Two lugs, L^1 and L^2, are screwed into the holder H about 110° apart at the exterior circumference of the rings, and serve as bearings for the rings in rotating. Two stops, RS^1 and RS^2, the former only of which is shown in the blueprint, are attached to the convex cylindrical surface of the rings as bearings for the yoke Y, by the action of which the rings are rotated. This yoke is moved by a lever L connected with the yoke by a free double-pointed pin P and by the spring Sp^2, which serves to keep the points of P in their respective cup bearings. The direction of movement of Y is tangential to the rings. A spring Sp^1 is attached to hooks affixed to the convex surfaces of the rings, so that the stops RS^1 and RS^2 are always held snugly against the tips of Y. Thus any movement of the yoke moves the gratings through an equal angle.

The longitudinal movement of the yoke Y is limited by the position of two stops, St^1 and St^2. St^1 is made with a long threaded sleeve, through which passes the shaft of the micrometer screw Scr. The base of this stop is quite wide, and bears on the plane surface of the holder H with its entire nether surface. Its tendency to rotate with the screw is thus made negligibly small. The sleeve of St^1 passes through a circular opening in Y the center of which is in the axis of the screw and of Y. The fit is rather close, just permitting free longitudinal movement of Y over the sleeve. The stop St^2 limits the movement of Y in the opposite direction. The base of this stop also bears on the plane surface of H. The shoulder of St^2 against which Y is drawn is made with a circular opening large enough to permit clear passage of the shaft of Scr and easy passage of the sleeve of St^1. The base of St^2 carries two slots, through which pass two strong screws that fasten St^2 to the holder H at the setting desired. To change the setting of St^2 these screws are loosened, St^2 drawn against Y, and the whole moved by the micrometer screw until St^2 reaches its proper position. Then the screws are tightened and the yoke

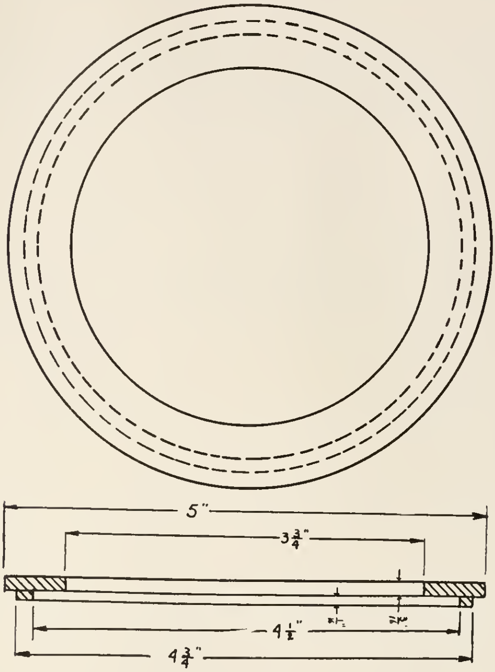

5"
3 3/4"
1/8"
4 1/2"
4 3/4"

FIG. 4-a

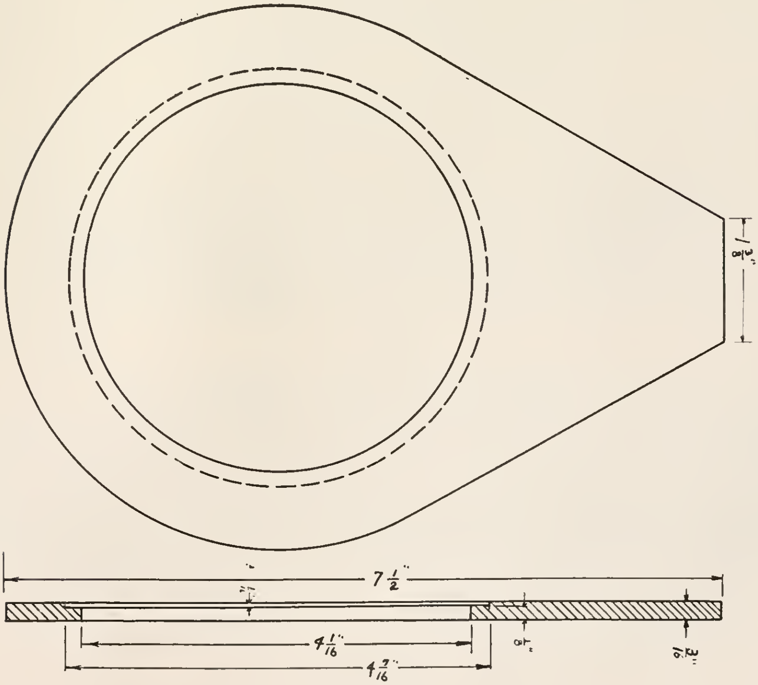

1 3/8"
7 1/2"
1/8"
4 1/16"
4 7/16"
3/16"

FIG. 4-b

Construction drawings for mountings.

and St¹ withdrawn. The head of the micrometer is calibrated to read to 0.02 mm. Readings to 1 mm. are made directly from the scale Sc. The journal bearing J for the micrometer screw and the lugs L¹ and L² carry shoulders on which the upper surface of ring R¹ bears. The corresponding surface of the (inverted) ring R² bears on the plane surface of H. As shown in the construction drawings, the rings carry shoulders from their convex cylindrical surfaces. The limbs of Y move in the groove formed by these shoulders, while the sleeves of St¹ fits snugly in the cir-

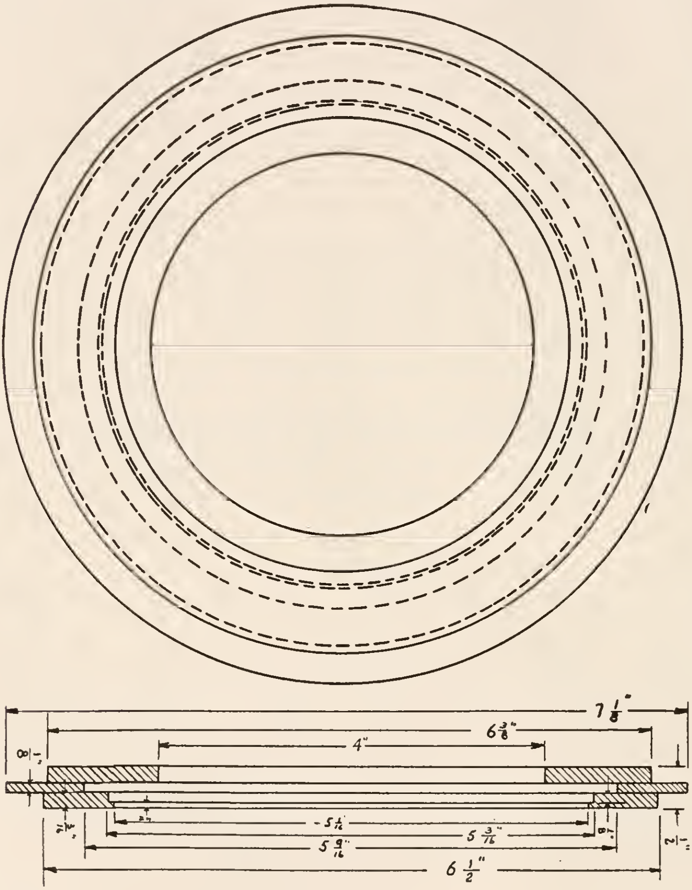


FIG. 4-c
Construction drawings for mountings.

cular openings of St^2 about the axis of Y. All movement of Y except in the direction longitudinal to the axis of Scr is minimized. The spring Sp^1 by its constant action against Y, assures that all resistance to the micrometer screw is made against one face of the threads. The micrometer readings are therefore highly accurate. The holder H, carrying the parts just described, is fitted in a ring B, flanged as shown in the construction drawings, so as to permit of free rotation about an axis normal to its plane surfaces, within limits determined by the setting of two stops, BS^1 and BS^2, attached to the rim of B. A 360° scale is divided on B, on which, from the indicator I, the direction of the test-bands may be read. This feature is useful for making quick and measurable changes in the direction of the test-bands between two given settings. When it is not needed, H can be secured so that the test-bands lie in any desired direction, by the action of the set-screw SS, which bears against the convex cylindrical surface of B.

All the metal parts are of acid-blackened brass, except the two springs, the pin P, the millimeter scale and the shaft of the micrometer screw. These are of steel. Three weeks were required to make the mountings for the two instruments. The gratings used are ruled 240 lines to the inch. The ruled lines, which are filled with an opaque substance, are of the same width as the clear interspaces. The gratings are obtainable from Max Levy of Philadelphia at $18.00 the pair.

As appears in Behn's formula, the grating width being given the separation of the test-bands varies inversely as twice the sine of half the angle of rotation. The scale-reading on the present instrument divided by 59 (half the distance in millimeters from tip to tip of Y) gives the tangent of half this angle. In the present work it is not necessary to correct for the cosine factor, since the angle used is so small that the sine and tangent are practically equivalent.

In the present work the writer is using a cheap substitute for the double photometer-box recommended by Yerkes and Watson. Two instruments are used, so that the Yerkes-Watson stimulus-adapter is unnecessary. In each compartment of the double photometer-box is placed a wooden track on which rests a carriage with a 60-watt tungsten lamp, protected by suitable diaphragms. A screen of two superposed panes of opal flashed glass is placed close behind the test-object, the latter being screwed into the end of the photometer box before a window of suitable size. The brightnesses of the two test-fields are made respectively equal, each being balanced against a standard lamp. The apparatus is so arranged that the test objects are brought directly before, and close to, the corresponding windows of the Yerkes box. These windows are further limited by acid-blackened brass plates, in each of which a circular window 6 cm. in diameter has been accurately cut and beveled, and carefully centered with respect to the test-object and the ends of the alley to which it belongs.

To present test-bands of a given size, stop St^1 is set in the desired position by the micrometer screw. If stop St^2 be set at a considerable distance (15 mm. for the present gratings) from St^1, the experimenter can cause the striae to disappear by moving the yoke Y against St^2, since this increases the angle of rotation enough to reduce the striae to the order of the ruled lines on the gratings. This change can be made from the experimenter's chair, by merely pulling a string attached to the lever L. When the string is released the spring Sp^1 brings the gratings to their former position. If one desires to shift from one size of visible striae to another, as for work in Problem 2 suggested above, the setting of St^2 is of course changed so as to limit the movement of Y to the desired degree in that direction.

The above procedure has been used successfully in problems 1, 2 and 3, with quite satisfactory results. The writer has one suggestion to make as a result of his experience: the grating-width 1–240 inch is satisfactory for work with the human subject, and with animals whose visual acuity is 50% poorer. It can be used at ordinary reading distance, if necessary, but for animals should be placed considerably farther from the eye. For animals whose vision is relatively poor the grating is too fine. It is impossible to present striae whose width is greater than 4 mm. without inconvenience where the distance from eye to test field is less than a meter. The angle of rotation at this reading is so small that disturbance from parallax results at short distances. Further where the angle of rotation is very small, very slight changes in the setting of St^1 cause changes in the width of the test-bands which are inconveniently large. In work on the chick in Problem 2, the range of widths of the test-bands is not long enough for extensive work, although the gratings were satisfactory for Problems 1 and 3. I should recommend, therefore, that the investigator provide a second set of gratings, of say 1–100 inch width for use on animals whose vision is poorer than that of the chick. The extra set of gratings can be cemented into their own rings, and would thus be made quickly interchangeable with the finer set.

For testing the threshold for contrast, the writer has had two special Lummer-Brodhun cubes of 6 cm. square face, constructed as shown in Fig. 5. These cubes are obtainable from Schmidt & Haensch at about 490 marks the pair. About two months' time is required for manufacture. The pattern etched on the diagonal face is three bands, each 1 cm. wide and 8.42 cm. long, the clear portion lying between any two of the etched bands being of the same size. The cubes, C^1 and C^2, are set a little back of the windows, W^1 and W^2, of the Yerkes box, in which the animal is placed. L^1, L^2, L^3 and L^4 represent the stimulus-lamps, and Sc^1, Sc^2, Sc^3 and Sc^4, opal-glass diaphragms, indicated in the sketch but not lettered, are used to protect the cubes and the windows of the Yerkes box from reflected light. D^1, D^2, D^3, and D^4 represent sectored discs. D^1 and D^2 as a pair are interchangeable with D^3 and D^4 as a pair. The portions of the fields illuminated by each lamp are equalized in brightness by placing

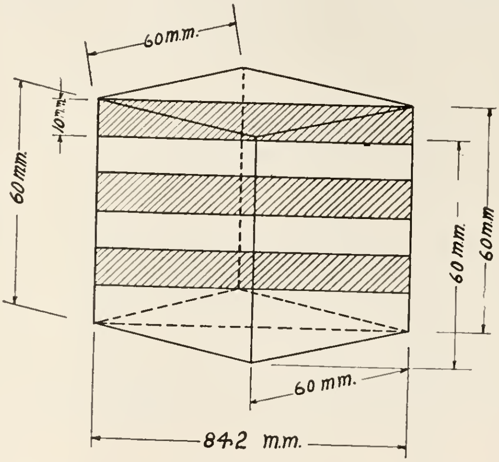


FIG. 5. Special Lummer-Brodhun cube showing pattern.

the lamp, which rests on a wooden photometer track. Each lamp, it may be seen, illuminates an equal area on the cube to

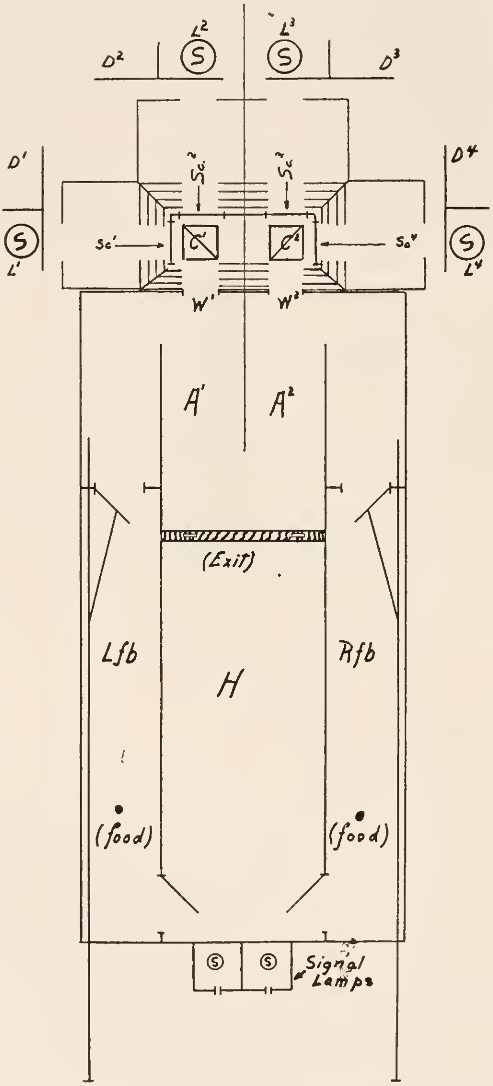

L^2
L^3
D^2
D^3
S
S
D^1
D^4
Sc^2
Sc^3
Sc^1
Sc^4
C^1
C^2
S
S
L^1
L^4
W^1
W^2
A^1
A^2
(Exit)
Lfb
Rfb
H
(food)
(food)
S
S
Signal Lamps

FIG. 6. Floor plan of Yerkes box, arranged for contrast-discrimination

which it belongs. The sectors D^1 and D^2 each have an angular opening of 180°. Thus the face of the cube which they illuminate will have a uniform surface-brightness. The angular opening of D^3 is $180+n°$, and that of D^4, $(180-n°.)$ The luminous intensity of this field is therefore equal to that of the plain field, but this field appears striate, the degree of contrast between the dark and the bright portions depending on the value of n. Interchange of D^3 and D^4 with D^1 and D^2 reverses the relative positions of the plain and the striate fields. Diaphragms placed between the cubes and the windows of the Yerkes box limit the visual field as closely as possible to the surfaces of the cubes.

I have not yet used this apparatus in actual tests, and some questions of convenience have yet to be settled. One of these is a suitable means of effecting a quick and noiseless interchange of the two pairs of sectors. Another important question is the rate of speed at which the sectors have to be driven. At the suggestion of Director Hyde of this laboratory I have decided to postpone tests on contrast-sensitivity until the threshold for rate of flicker under the experimental conditions shall have been ascertained for each individual subject.

Having ascertained experimentally, however, that certain animals under the experimental conditions can distinguish striae narrower than those on the cubes when the contrast is sharp, the writer assumes without scruple that a method of preparing the stimuli which meets physical requirements for that purpose should show what degree of contrast is necessary to arouse such discrimination.

VISUAL PATTERN-DISCRIMINATION IN THE VERTEBRATES—II

COMPARATIVE VISUAL ACUITY IN THE DOG, THE MONKEY AND THE CHICK

H. M. JOHNSON
Nela Research Laboratory,
National Lamp Works of General Electric Company

In an earlier paper[1] the present writer discussed the question of discrimination of visual detail in animals, in its bearing on other problems of vision, and on that of vision as a factor in evolutionary theories. In attacking experimentally the four elementary problems suggested in that paper, the first question to be settled is, how large must the pattern be, the degree of contrast being given, in order for the animal to distinguish the pattern from a plain field, having the same area, form, range of wave-lengths and luminous intensity as the field on which the pattern appears. This information is necessary before one may safely assume that two patterns to be discriminated one from the other, are both distinguishable as such. The pattern to be distinguished from the plain field in the present work is simply a series of horizontal black and white striae of equal width with respect to each other, but whose absolute width may be varied by insensible gradations from invisibility to marked coarseness without changing any other stimulus-factor.

The writer chose as subjects the dog, the monkey and the chick (Gallus domesticus). The choice was dictated partly by an interest in the relation between visual acuity and the structure of these different types of eyes, and partly by a desire to add further data to those already accumulated by other students in other problems of vision in these animals. The present work (on pattern-vision in general) promises to extend over a considerable period of time, and it seems best to publish the results in a series of separate papers as individual problems are completed. In a later communication I hope to discuss some results obtained by other students in the light of results of the present work.

---

[1] "Visual Pattern-Discrimination in the Vertebrates." I. Problems and Methods. This Journal, vol. 4, 1914, pp. 319ff.

As is well known, the dog's eye is very imperfect in some respects. The imperfections are not so much those inherent in his eye as a refractive system as those of lack of development and imperfect functioning of other parts. According to Slonaker[2], the dog's eye possesses no fovea, and even the " sensitive area " is not well defined. Slonaker was unable to demonstrate a round " sensitive area " slightly temporal to the nerve entrance, which Chievitz described; and he mentions the disposition of the blood-vessels as indicative that the area is band-like. The pupillary opening is always large; the response to light is fairly quick but not strong; movements of rotation are very slight. The writer has demonstrated convergence in several individuals, however.

The monkey's eye, like those of the other primates below man, possesses a well defined, round " sensitive area," and a well developed fovea centralis (slightly temporal to the nerve-entrance) of medium depth, as measured in the number of layers of cells. The pupillary opening is small in strong light; responses to light are quick and strong; pupillary changes apparently accompanying changes of accommodation are marked. There is unmistakable convergence; rotatory movements are coordinate, but are more limited in range than are those of the human eye. This is probably due to the fact that the orbit is deep and the eyes are set rather deeply in it.

The chick is said by Slonaker to have so shallow a depression as to be very doubtful; he found only a slight thickening in the region where Chievitz reports an area nasalis and a questionable fovea nasalis. Birds in general are characterized by the presence of a fovea, and in some species, such as the tern and the sparrow-hawk, there are two; one temporal and one nasal. The temporal fovea may be regarded as a modification of the fovea centralis, considerably displaced. Due to the position of the eyes in the head, some birds which possess it cannot make close convergence. By dilating the pupil it is possible to image an object lying directly in front of the bird, on to both temporal foveas simultaneously, without much convergence. Objects placed laterally to the bird may be imaged on the nasal fovea and are often, if not usually, regarded monocularly. The chick is thus not fairly representative of birds as a class. Its eye shows convergence, and pupillary changes under conditions of varying illumination and varying accommodation are marked. Movements of rotation except for convergence are slight, however, and seldom made.

---

[2] Slonaker, J. R., "A Comparative Study of the Area of Acute Vision in Vertebrates," *Journal of Morphology*, vol. 13, 1897, pp. 448 ff.

As has been mentioned, the two test-fields for this problem were both striate, in the horizontal direction. On the standard field the individual striae were about 0.11 mm. wide, and it was assumed that at the distance given they were too small to be resolved by the eye. On the variable field, which was interchangeable with the standard field, the striae were larger, the actual size in millimeters for each day of the experimentation being shown in the accompanying tables. The test-fields were prepared by using two pairs of superposed gratings, mounted as described in the paper by the present writer cited above. Each field was limited by a circular window 6 cm. in diameter, beveled in an acid-blackened brass plate, which was placed behind the window of the Yerkes experiment-box, with the test-object close behind it. The test-objects were mounted at the windows in the end of a two-compartment photometer-box, essentially like that described by Yerkes and Watson.[3] Behind each test object, in the compartment belonging to it, was mounted a 60 watt Mazda lamp, whose carriage rested on the photometer track. Between each lamp and the test-object which it illuminated was placed a diffusing screen of opal flashed glass, protected from reflected light by diaphragms, and fixed to the track close behind the test-object. The lamps were connected in multiple and burned at normal voltage, the current being taken from a system of 25-ampere storage cells. A voltmeter and rheostat connected in series with the lamps enabled the experimenter to keep the current constant. The test-fields were equated in brightness by placing the lamps; their brightness was determined by the use of a Sharp-Millar photometer, as 12.24 candles per square meter. Considered as sources each field had a luminous intensity of 0.034 candles in the direction normal to its surface. The brightness used is a comfortable reading condition for the human subject. We have no reason for assuming that it was or was not optimal for any of the animals used. It will be remembered that each test-object could be made to present a sensibly uniform or a sensibly striate field by changing the angle of rotation of the gratings over each other. This change is made between limits determined by the setting of two stops with a micrometer screw, by moving a lever attached to the mounting. Change of the size of the striae does not alter the mean brightness of the field. Hence the test-objects are not interchanged when it is desired to interchange the fields, and any changes in brightness, range or relative intensities of wave-lengths, odors, etc., which a test-object might suffer, could not aid the animal in forming a discrimination habit. They would be presented with the negative field as often as with the positive field. For this reason repeated photometric measurements are unnecessary. It is unlikely that any changes take place save the decline in efficiency of the lamps, which progresses slowly and at a fairly uniform rate between wide limits. The writer observed no sensible changes in the experimental conditions during the work on this problem.

---

[3] Yerkes, R. M., and Watson, John B., "Methods of Testing Vision in Animals," *Behavior Monographs*, vol. 1, No. 2, 1911.

In these experiments I used the well-known discrimination method, combining the motives of punishment and reward. By referring to Fig. 6 of the earlier article cited, the reader may see the floor plan of the Yerkes box which I used. Food was placed in both food-compartments, Rfb and Lfb. Entrance to the food-boxes had to be made through alleys A^2 and A^1 respectively, at the ends of which the respective test-fields appeared. Each of the alleys was floored with a punishment grill essentially like those described by Yerkes and Watson (op. cit. P.) and by Yerkes.[4] The grills were hinged to the floor of the box at the ends next the test-objects, and supported at the free end by a light spring. A rod passed through a sleeve fastened to the under side of the true floor of the box and was kept in contact with the under surface of the grill by means of the supporting spring. A mercury cup contact, insulated from the rod, was carried by the latter. The circuit through the signal lamps indicated in the figure was kept closed at this contact until the animal stepped on to the punishment grill and depressed it. This broke the circuit through that signal lamp, and enabled the experimenter to ascertain what choice the animal made without watching the animal in the act of choosing. I consider this feature important, since it enables the experimenter to avoid giving certain secondary cues to the animal. I adopted the device at the suggestion of Professor Watson, who had been using a similar one for some time. The entrance-doors to the food-boxes Rfb and Lfb are controlled by rods indicated in the diagram, which pass to the experimenter's station. These doors are kept closed against the animal until the latter shall have entered the proper entrance-alley, which fact is indicated by the signal lamp. After the animal has passed into the food-box, the entrance-doors are closed behind him, and he is readmitted to the home-box through another door opening directly into it. This door is also controlled by rods which are not indicated in the sketch. It is unnecessary for the experimenter to touch the animal during the daily series. Except for the light from the signal lamps passing through pin-holes made in the boxes in which the latter are placed, all the surroundings of the test-fields were dark when the stimuli were presented. (The walls and floors of the experiment-box are painted dead black.) This does not indicate conditions of dark adaptation, however. A 1 c.p. lamp with a frosted bulb is mounted in the top of each food-box. It is protected by a metal shield, so as to exclude direct light, as far as possible, from the animal's eye, and is so placed that the animal is turned away from it while eating. This lamp was not switched on until the animal had made his choice. Two such lamps were similarly mounted in the home-compartment H. They were switched on and the lamps in the food-boxes switched off, after the animal had finished eating and the settings had been made for the next trial. The lamps in H were switched off before the exit-door was opened. All the animals quickly learned to pass from the dark compartment into the illuminated one, as soon as the doors were opened, and without other attention from the experimenter.

---

[4] Yerkes, R. M., "The Dancing Mouse." N. Y., Macmillan, 1907.

The criterion of choice was the animal's entering a given alley. Should the animal enter the wrong alley he was not disturbed but was admitted to the proper food-box when he voluntarily entered the proper alley. The choice in such case, however, was recorded as incorrect. In this work the distance between the test-object and the animal's eye is a necessary factor. The experimenter prepared a number of stops extending across the compartment introductory to the alleys, and placed them so that the animal could not bring the eye nearer than 60 cm. to the test-object without overstepping the stop and stepping on to the punishment grill. The setting of the stop used was different for each animal. This rendered the accommodation-factor the same for each animal.

All the animals were punished for incorrect choices by placing inductive charges on the electrodes of the punishment grills. The current was taken from a 110 volt A. C. power circuit, a 100 watt lamp placed in another room being connected as resistance in series with the primary coil of a Zimmerman inductorium. The position of the secondary coil with reference to the primary could be varied at will, the setting being shown on a scale belonging to the instrument. There is much less disturbance with this arrangement than where D. C. is used with an interrupter. In previous work I found the noise from the interrupter quite disturbing, and the interrupter also worked uncertainly at times. In the first few weeks of this experimentation I charged the grill under the negative test-field before releasing the animal from the home-box. The circuit through the primary coil was kept closed throughout the daily series of trials. Later this arrangement was found quite unsatisfactory, as will appear in remarks on the behavior of the dog. I then changed the wiring so that the circuit through the primary was kept open until the animal closed it by stepping on the grill and thus depressing it. This prevents the animal from testing the two grills for charge, and acquiring a discrimination-habit on that basis, rather than on a visual one. The shock under the latter condition is quite different in character from that under the earlier conditions. Under the latter, there is a pronounced " inductive kick " at the instant the primary circuit is opened or closed. This is disturbing at first, but has one advantage: the animal tends to leave the alley at once, rather than remain on the grill and receive more punishment. The charge, of course, must be made considerably lighter than under the former set of conditions. Before each daily series of trials, I soaked the animal's feet for several minutes, so that they remained moist throughout the series. I could not use a wet pad in the box, owing to the character of the wood, which warps very easily. But the shock conditions remained as controllable as it was practicable to make them under the circumstances.

The levers by which the stimuli were interchanged were attached by strings running through a pulley-system to the handle of the double-throw switch which controlled the charge on the respective punishment grills. Thus, by merely turning the switch, the respective positions of the positive and negative fields were interchanged. It was thus made impossible for the animal to receive a shock under the positive test-object, or to avoid it if he stepped into the alley under the negative test-object. A further slight change in the apparatus would have made it safe in the hands of an inexperienced student. That is, installing a wiring system by which the entrance-doors to the proper food-compartment would open electro-magnetically when the animal entered the proper alley.

The order of presenting the standard field to the right or left of the variable field was determined before each series by the use of a well shuffled pack of twenty cards. The only exception to the rule of strict irregularity of presentation was that the two fields should not occupy the same position with respect to each other through more than three successive trials during the learning period, and not more than four successive trials during the advanced stages of discrimination. The animals practically never received the stimuli in the same serial order. Of course, in twenty trials the standard field would appear ten times to the right and ten times to the left of the variable field.

The following animals were used in the work herein reported:

Dog 1: a pure bred male English bull terrier; six months old at the beginning of the experimentation.

Monkey 1: an adult male Cebus, variety not established; purchased from a dealer. He died before learning the problem, but certain features of his behavior are noteworthy.

Monkey 2: a male Cebus, nearly full grown, but not sexually mature; variety not established; purchased from a dealer.

Chicks 1 and 2: both pure bred Indian gamecocks, six months old at the beginning of the experimentation; bred by Robert Stedman, Beachland, Nottingham, Cleveland, Ohio.

All of the animals were easily tamed, and none except Chick 1 showed any great excitability in the experiment-box. All were kept free in the same large, well-lighted room, steam-heated and with forced ventilation. The floor was kept covered with a layer of sawdust 2 inches thick, in the interest of cleanliness. All the animals, with two exceptions, remained in excellent condition throughout the work. Monkey 1 was active and playful on the morning of his death. The cause of death was not ascertained, but the most plausible guess is that he became overheated and fell to the floor from an overhead steam-pipe, on which he habitually slept. Chick 2 was the smaller of the two gamecocks and sustained severe injuries in fighting the other bird. On February 9, while in a crippled condition, he was also attacked by Dog 1 and sustained several deep scratches, some of which required several stitches. They were properly treated, however, and healed without infection, and without serious disturbance of the work.

The learning records of the different individuals appear in Tables 1 to 4, inclusive. Certain noteworthy features of the behavior of the different animals must be noted separately.

The dog's learning record up to and including January 7, when the problem ordinarily would be regarded as " learned " is unusual. Up to the introduction of punishment he was not affected by the stimuli. From the day when punishment became effective the learning curve descends abruptly, showing very short plateaux and no reversals . This, as far as I have observed, is hardly characteristic of acquisition of a discrimination-habit. An earlier (unpublished) experiment of mine on visual form-discrimination in the dog, which I expect soon to describe in another report, and the behavior of some blind dogs which I worked[5] in comparison with normal dogs, tended to make me suspicious of this dog's record. At the time, however, I could find nothing to warrant the suspicion, and in good faith I reported the dog's results[6] as indicating that the method of making such tests is reliable. On January 26, after the test-bands had been reduced to about 40% their original size, I noticed that the dog sniffed several times at the entrance of each alley before he made his choice. Dogs under conditions of excitement often sniff apparently to release surplus energy, but this animal was making perfect records and did not show any other forms of excitement.

---

[5] Johnson, H. M., "Audition and Habit-Formation in the Dog," *Behavior Monographs*, No. 8, 1913.

[6] "A Method of Testing Visual Acuity and Pattern-Discrimination in Animals," *Psychological Bulletin*, vol. 11, 1914, pp. 55 ff.

It is clear that sniffing for odorous food-substances could serve no useful purpose, as food was present in both food-compartments. It occurred to me that the dog might be testing the punishment grills for charge in some way, and choosing the alley whose floor was not charged. I therefore introduced an additional key in the secondary circuit, so as to leave both grills uncharged until the dog should step on to the wrong one, when I would close the circuit by hand. As the record shows, the suspicion was well grounded. The animal's subsequent records weaken the supposition that the animal had ever been discriminating on a visual basis. I now changed the wiring so that the circuit through the primary is left open until the animal closes it automatically by stepping on the wrong grill. Throughout the rest of the work, on each individual, I took the additional precaution of testing the secondary circuit with the fingers before each trial, to make sure that the primary circuit was open. The tungsten-mercury contact would occasionally fail to break.

The nature of the dog's test for charge is an interesting question. It is improbable that he was touching the electrodes with his nose. That happened once or twice in the preliminary stages of the work, and the reaction was negative and violent. At this stage the signal-lamps did not flicker save when he stepped on to the grill. Unipolar stimulation of the nose is possible, but it is hard to suppose that he could control his movements accurately enough to avoid bipolar stimulation while seeking unipolar stimulation. The current used was not strong enough to be markedly unpleasant to the moistened human fingers, but the dog usually howled when he received it through his wet foot. His nose is always damp, and is apparently more sensitive to shock than the foot. I ascertained that his vibrissae are too short for him to touch the electrodes with them without bringing the nose or lips uncontrollably near. They or the hair about the lips might have been so affected by the electric field as to give a sensory response, but in this connection it is well to note that they were usually wet. Dr. Lorenz of this laboratory was kind enough to go over the situation with me when I consulted him regarding the possibility of ozone or some odorous gas similarly generated being in the charged field. He informs me that with the difference of potential which in this case existed between the charged electrodes, ozone in minute quantities would certainly be present. It therefore seems possible that the dog was reacting to olfactory stimulation from ozone or some other odorous gas formed in the charged field. Bearing in mind his pronounced sniffing behavior, this seems the simplest explanation.

The sniffing responses persisted for a long time and were never entirely overcome. After this change in the wiring in over 67% of the times when the animal sniffed during a trial the choice was wrong.

The evidence obtained in this work is not conclusive against the dog's possessing sensitivity to visual detail. The fact that this individual learned to control his environment for a time by the use of smell may have unfitted him in part for visual discrimination. And yet the other animals acquired it more or less easily. I have obtained another individual which is to be put to work on the same problem, along with a cat, in order to throw light on the question whether the carnivora have poor vision, or whether the test made on this dog was unfair to him. I may add that the present gratings are too fine for satisfactory work with the dog. They do not permit test-bands wider than 4 mm. to be used satisfactorily. Above that value, parallax is present, and the angle of rotation is very small, so that a very small change in the setting of the micrometer screw produces a very large change in the width of the test-bands. If an animal's threshold lies in this region the steps which can be taken are too large for convenience.

Both the monkeys used were very active in the experiment-box. When I introduced punishment in the tests on Monkey 1 he had been maintaining an accuracy record of 80% for several consecutive daily series of trials. His responses were made without comparison, however. Punishment was not satisfactory. At this time the grill forming the floor of the alley under the negative test-field carried an induced charge all the while the stimuli were being presented. In one sense the charge was not unduly heavy. The animal would frequently sit on the charged grill for several minutes, chattering, and picking at different parts of his body. Occasionally he would touch the grill with his hand, give a sudden, though not loud, exclamation, and put his fingers into his mouth. But he showed a decided aversion to touching the grill while choosing, and developed numerous methods of getting through the alley without doing so. I had not succeeded in circumventing all these methods at the time of his death. Monkey 2 developed a similar tendency. I never used a charge heavy enough to make him tend to avoid the alley where he was last shocked. When I introduced punishment into the work on him I had already changed the wiring of the box as described above. He has taken one of the grills by the free end and depressed it ten or twelve times in rapid succession uttering a slight exclamation at each shock. And yet he avoided touching them while making a choice. The long breaks in his record prior to March 11 are due to the necessity of modifying the box so as to limit his movements. The change which finally proved effectual was installing a removable wooden partition extending across the box at the entrance to alleys A^1 and A^2 from floor to ceiling. It contained two windows each 4 inches square, so placed that its axis coincided with that of the test-object at the other end of the alley. The animal crawled slowly through the window at each trial and dropped on to the grill. The position of the windows permitted the animal to view the test-objects normally but prevented him from viewing them simultaneously as the dog and the chicks could do. This was undesirable, and at the suggestion of Professor Watson I substituted for the wooden partition one made of plate glass 1-4 inch thick containing circular windows 4 inches in diameter corresponding to those in the wooden partition. The change caused no disturbance. As the test-bands were reduced in width to the point where discrimination became difficult, the monkey would come to the partition and bring his head before first one opening and then before the other in rapid succession. In the latest stages of work on this problem he would sometimes peer through a given opening two or three seconds. In the earlier stages he apparently regarded the stimuli through the plate glass, and his movements were very rapid.

It has probably occurred to the reader that it was possible for this animal to extend his head several inches through these windows without dropping on to the grill. Thus he could bring his eye nearer to the test-object than the 60 cm. distance which the partition fixed. This would have introduced a variable factor hard to control. Until May 7 I did not watch the animal in the act of choosing, but his movements were so rapid that I could follow them by the noises he made with fair accuracy.

Usually only a very short fraction of a second would elapse between the noise of his rubbing against the window and the flicker of the signal lamp. But as his responses became slower I began watching him through a crack in the top of the box, and continued from May 7 to the end of the tests. Between the 7th and the 13th of May this irregularity never occurred; between the 13th and the 31st, in a total of 360 trials, it occurred five times. That is, the animal would extend his head and sometimes part of his body through the window opening into the wrong alley, and then reverse the choice without dropping on to the grill. Each time I threw out the choice so made and repeated the trial elsewhere in the series; four times the repetition resulted in a correct choice and once incorrect. This shows that the distance-factor is very constant and reliably controlled even in the case of the monkey.

I found that the monkey was not disturbed by occasional visitors when the latter were seated in an inconspicuous place. For the purpose of getting suggestions as to possible secondary sources of error I conducted several series of tests in the presence separately of Dr. Cobb, Dr. Worthing, Mr. Cady and Mr. Luckiesh of the research staff of this laboratory, and Dr. Breitenbecker of the Western Reserve University.

Chick 1 is an unsatisfactory animal for this work because of extreme excitability. It was difficult to control the current used as punishment so as to affect him at all without so disturbing him as to render him unfit for work. The learning record in Table 3 shows that I did not always succeed in this particular. Several times I had to remove him from the box and leave him for 24 hours without food, in order to obtain responses. At other times a rest of several days seemed necessary. However, it was possible, by re-training him at larger stimulus-values, to overcome such disturbances for the time, and he actually yielded a slightly lower threshold than did Chick 2, who was a much better subject. The learning record of the latter I consider quite good.

Reduced to terms of visual angle subtended by individual striae, the values taken as the stimulus-threshold are for Chick 1, 4′ 04″; for Chick 2, 4′ 14″; for Monkey 2, 57″. Generally speaking, such “ threshold-values ” obtained by the discrimination should not be construed too rigidly. They certainly are not

TABLE I

RECORD OF DOG 1

Date	Width of striae (mm)	Number of trials given	Number of correct choices	Remarks
Dec. 10	2.230	8	4	Refused to work after trial (7).
“ 11	2 230	10	4	Refused to work for three hours.
“ 12	2.230	16	7	
“ 13	2.230	16	4	Invariable choice of Rfb.
“ 14	2.230	16	8	Preference for Rfb.
“ 15	2.230	16	6	
“ 16	2.230	10	2	Invariable choice of Rfb.
“ 17	2.230	10	3	Invariable choice of Rfb. Light charge on grills.
“ 18	2.230	10	3	Invariable choice of Rfb. Charge increased.
“ 19	2.230	10	3	Invariable choice of Rfb. Charge increased further.
“ 20	2.230	15	6	Position habit interrupted.
“ 21	2.230	10	4	Preference for Rfb; disturbed by punishment.
“ 22	2.230	10	6	Preference for Rfb; disturbed by punishment.
“ 23	2.230	10	8	No position preference.
“ 24	2.230	10	9	
“ 25	2.230	10	9	
“ 26	2.230	10	9	
“ 27	2.230	10	10	
“ 28	2.230	10	10	
Jan. 7	2.230	10	10	
“ 8	2.230	10	10	
“ 9	2.230	10	9	
“ 10	2.230	10	10	
“ 11	2.230	10	10	
“ 12	2.230	10	10	Considered ready for stimulus-threshold tests.
“ 13	2.168	10	10	
“ 14	2.138	10	8	
“ 15	2.138	10	9	
“ 16	2.138	10	3	Great disturbance at punishment; behavior ambiguous.
“ 16	2.138	10	9	Made as control test three hours later.
“ 17	2.138	10	8	
“ 18	2.138	10	10	
“ 19	1.951	10	10	
“ 20	1.951	10	8	
“ 21	1.951	10	10	
“ 22	1.735	10	9	
“ 23	1.735	10	10	
“ 24	1.561	10	10	
“ 25	1.419	10	10	
“ 26	1.419	10	10	First appearance of sniffing reaction; see note.
“ 27	1.301	10	10	Sniffing pronounced; see note.
“ 28	1.301	10	7	Control-test; method of giving punishment changed.
“ 29	1.301	10	4	
“ 30	1.561	10	7	
“ 31	1.561	10	4	
“ 31	2.230	10	5	
Feb. 1	2.230	15	7	
“ 3	2.230	10	7	Not worked previous day; box being altered.
“ 4	2.230	10	4	

TABLE 1—*Continued*

Date	Width of striae (mm)	Number of trials given	Number of correct choices	Remarks
Feb. 5	2.230	10	2	
" 6	2.230	15	10	
" 7	2.230	10	5	
" 8	2.230	10	5	
" 9	2.230	10	5	
" 10	2.230	10	5	
" 11	2.230	10	4	Regarded as not being affected by stimulus-difference.
" 12	7.804	10	2	
" 13	5.204	10	5	Size of striae reduced to avoid parallax disturbance.
" 15	5.204	10	5	Sniffing habit interrupted.
" 16	5.204	10	8	Sniffed three times; made two wrong choices.
" 17	5.204	10	9	Sniffed at one trial; chose wrong alley.
" 18	5.204	10	9	Sniffed at one trial; chose wrong alley.
" 19	3.902	10	3	Disturbed by punishment; preference for Rfb.
" 20	3.902	10	6	Preference for Rfb; no sniffing.
" 21	3.902	10	7	
" 22	3.902	10	5	
" 23	3.902	10	6	
" 24	3.902	10	7	
" 25	3.902	10	8	
" 26	3.902	10	6	
" 27	3.902	10	7	
" 28	3.902	20	11	
Mar. 1	3.902	20	15	Sniffed at two trials; both choices wrong.
" 2	3.902	10	6	No sniffing.
" 3	3.902	10	7	
" 4	3.902	10	5	Invariable choice of Rfb; punishment increased.
" 5	3.902	10	4	Preference for Rfb; greatly disturbed by punishment.
" 9	3.902	10	8	No position preference; less excitable than before rest.
" 10	3.902	10	8	
" 11	3.902	10	8	Considered ready for control.
" 11	3.720	10	5	Sniffed at three trials after making two errors; both choices wrong.
" 12	3.720	10	7	
" 13	3.720	10	8	
" 14	3.720	10	8	
" 15	3.720	15	12	Preference for Rfb; punishment increased.
" 16	3.720	10	5	Preference for Rfb.
" 17	3.720	10	4	Preference for Rfb.
" 18	3.720	10	8	Preference for Rfb.
" 21	3.720	10	6	No work since 18th; preference for Rfb.
" 23	3.720	10	8	Not worked previous day; preference for Rfb.
" 24	3.720	10	8	Preference for Rfb.
" 25	3.720	10	8	Preference for Rfb.
" 26	3.720	10	7	Preference for Rfb.
" 27	3.720	10	7	No position preference.
Apr. 5	3.720	10	5	
" 6	3.720	10	8	
" 7	3.720	10	5	

TABLE 2

RECORD OF MONKEY 2

Date	Width of striae (mm)	Number of trials given	Number of correct choices	Remarks
Jan. 26	2.230	10	7	Not punished.
“ 27	2.230	10	7	
“ 28	2.230	10	4	Invariable choice of Lfb.
“ 29	2.230	10	5	Preference for Lfb.
“ 30	2.230	10	2	Punishment introduced. Avoided grills; removed.
Feb. 1	2.230	10	5	
“ 3	2.230	10	4	Responses slow.
“ 4	2.230	2	1	Avoided grills; removed.
Mar. 11	2.230	10	8	First day with wooden partition.
“ 12	2.230	10	4	Preference for Lfb.
“ 13	2.230	10	8	Punishment introduced and continued thenceforth.
“ 14	2.230	10	7	Preference for Rfb.
“ 15	2.230	10	5	Preference for Rfb.
“ 16	2.230	10	7	Preference for Rfb.
“ 17	2.230	10	4	Preference for Rfb.
“ 18	2.230	10	5	Preference for Rfb.
“ 19	2.230	10	5	No position preference.
“ 20	2.230	10	6	Preference for Lfb.
“ 21	2.230	10	6	Preference for Lfb.
“ 22	2.230	10	5	Preference for Rfb.
“ 23	2.230	10	6	Preference for Rfb.
“ 24	2.230	10	5	Preference for Lfb.
“ 25	2.230	10	7	Preference for Rfb.
“ 26	2.230	10	6	Preference for Rfb.
“ 27	2.230	10	7	Preference for Rfb.
“ 28	2.230	10	7	Preference for Rfb.
Apr. 4	2.230	10	9	No position preference.
“ 5	2.230	10	9	
“ 6	2.230	10	10	
“ 7	2.230	10	10	
“ 8	2.230	10	10	Not worked again until 14th.
“ 14	2.230	10	9	
“ 15	2.230	10	9	
“ 16	2.230	10	10	
“ 17	2.230	10	10	
“ 18	1.951	10	9	
“ 19	1.951	10	9	Ate little; responses slow.
“ 20	1.951	10	10	Glass partition used henceforth.
“ 21	1.951	10	10	
“ 22	1.735	10	10	
“ 23	1.561	10	10	
“ 24	1.419	10	10	
“ 25	1.301	10	10	
“ 26	1.201	10	10	
“ 27	1.115	10	10	
“ 28	1.041	10	9	
“ 29	0.975	10	10	
“ 30	0.940	10	10	
May 1	0.867	10	10	
“ 1	0.822	10	10	
“ 2	0.781	10	10	

TABLE 2—*Continued*

Date	Width of striae (mm)	Number of trials given	Number of correct choices	Remarks
May 2	0.743	10	10	
" 3	0.710	10	10	
" 3	0.679	10	9	
" 4	0.650	10	8	
" 4	0.624	10	10	
" 5	0.600	10	10	
" 5	0.578	10	8	
" 6	0.558	10	10	
" 6	0.538	10	10	
" 7	0.520	10	9	
" 7	0.504	10	10	
" 8	0.488	10	9	
" 8	0.473	10	9	
" 9	0.459	10	10	
" 9	0.441	10	9	
" 10	0.434	10	10	
" 10	0.422	10	10	
" 11	0.411	10	10	
" 11	0.400	10	8	
" 12	0.390	10	8	
" 12	0.381	10	9	
" 13	0.372	10	10	
" 13	0.363	10	10	
" 14	0.355	10	10	
" 14	0.347	10	9	
" 15	0.339	10	10	
" 15	0.332	10	9	
" 16	0.325	10	10	
" 16	0.318	10	10	
" 17	0.312	10	9	
" 17	0.306	10	8	
" 18	0.300	10	10	
" 18	0.294	10	8	
" 19	0.289	10	10	
" 19	0.284	10	9	
" 20	0.279	10	10	
" 20	0.274	10	9	
" 21	0.269	10	9	
" 21	0.264	10	10	
" 22	0.260	10	10	
" 22	0.256	10	9	
" 23	0.252	10	10	
" 23	0.248	10	10	
" 24	0.244	10	10	
" 24	0.240	10	8	Ate little and responded slowly.
" 25	0.236	10	10	
" 25	0.233	10	10	
" 26	0.230	10	10	
" 26	0.226	10	10	
" 27	0.223	10	10	
" 27	0.217	10	10	
" 28	0.211	10	9	
" 28	0.205	10	8	

TABLE 2—*Continued*

Date	Width of striae (mm)	Number of trials given	Number of correct choices	Remarks
May 29	0.200	10	9	
" 29	0.195	10	6	Responses slow; ate little.
" 30	0.195	10	9	
" 30	0.190	10	9	
" 31	0.185	10	9	
" 31	0.181	10	10	
June 1	0.177	20	15	
" 2	0.173	10	10	
" 2	0.169	10	10	
" 2	0.169	10	10	
" 3	0.166	10	8	
" 3	0.163	10	6	
" 3	0.260	10	9	
" 4	0.260	5	5	
" 4	0.163	10	7	Taken as threshold; subtends 57″ of V. A.
" 4	0.160	10	6	

TABLE 3

RECORD OF CHICK 1

Date	Width of striae (mm)	Number of trials given	Number of correct choices	Remarks
Dec. 17	2.230	10	4	In general room illumination.
" 18	2.230	10	4	Very light charge on punishment grills.
" 19	2.230	10	3	
" 20	2.230	10	5	Learned to leap from charged grill into entrance of food boxes.
" 21	2.230	10	4	Additional grill placed in entrances to food boxes.
" 22	2.230	10	2	
" 24	2.230	10	6	Preference for Rfb; not worked previous day.
" 25	2.230	10	4	Tendency to choose in rhythmic alternation.
" 26	2.230	10	5	Tests discontinued until January 7.
Jan. 7	2.230	10	5	This and succeeding series in darkness. No punishment.
" 8	2.230	10	5	Preference for Rfb; very slow, no punishment.
" 9	2.230	10	7	Preference for Rfb; no punishment.
" 10	2.230	10	7	No punishment.
" 11	2.230	10	5	Preference for Rfb; no punishment.
" 12	2.230	10	4	Light charge on punishment grills.
" 13	2.230	10	5	Charge increased; no effect.
" 14	2.230	10	4	Very much slower; tendency to stand on charged grill.
" 15	2.230	10	3	Responses very slow; charge reduced.
" 17	2.230	10	4	Invariably choice of Rfb.
" 18	2.230	10	3	Preference for Rfb.
" 19	2.230	10	7	Position habit interrupted by punishment.
" 20	2.230	10	3	Very slow.
" 21	2.230	10	8	

TABLE 3—*Continued*

Date	Width of striae (mm)	Number of trials given	Number of correct choices	Remarks
Jan. 22	2.230	10	3	Very slow.
“ 23	2.230	10	0	
“ 24	2.230	8	3	Refused to work after trial 8.
“ 27	2.230	10	4	Not punished; first work since 24th.
“ 28	2.230	10	4	Not punished.
“ 29	2.230	10	5	Not punished.
“ 30	2.230	10	9	Not punished.
“ 31	2.230	10	7	Light charge on grills.
Feb. 1	2.230	10	7	
“ 2	2.230	10	8	Disturbed by “inductive kick;” wiring recently changed.
“ 3	2.230	10	8	
“ 4	2.230	10	10	
“ 5	2.230	10	9	
“ 6	2.230	10	9	
“ 7	2.230	10	9	
“ 8	2.230	. .	. .	Refused to work; not fed; had fought most of day.
“ 9	2.230	20	14	Quite excitable; had been isolated in strange quarters.
“ 10	2.230	15	10	Still excitable.
“ 11	2.230	10	9	
“ 13	2.230	10	10	Not fed previous day; had refused to work.
“ 14	2.230	10	10	
“ 15	2.230	10	10	Considered ready for tests on stimulus-threshold.
“ 16	1.951	10	10	
“ 17	1.735	10	10	
“ 18	1.561	10	10	
“ 19	1.419	10	10	
“ 20	1.301	10	10	
“ 21	1.201	10	10	
“ 22	1.115	10	10	
“ 23	1.041	10	10	
“ 24	0.975	10	5	
“ 25	2.230	5	5	
“ 25	0.975	10	9	
“ 26	2.230	5	5	Refused to work when width of striae was reduced.
“ 27	2.230	5	4	Refused to work when width of striae was reduced.
“ 28	2.230	10	6	Refused to work for 20 minutes at first trial.
Mar. 1	2.230	10	10	Very excitable.
“ 2	2.230	10	10	
“ 3	2.230	10	9	Strong tendency to inhibit entrance to Lfb.
“ 4	2.230	10	10	Same tendency.
“ 4	0.975	10	6	
“ 5	2.230	10	10	
“ 6	0.975	10	7	
“ 9	2.230	10	7	
“ 11	2.230	10	10	
“ 12	2.230	10	10	
“ 12	0.975	10	8	Not punished.
“ 13	2.230	10	10	
“ 13	0.975	10	6	Tendency to choose last feeding-place; light charge on grills.

TABLE 3—*Continued*

Date	Width of striae (mm)	Number of trials given	Number of correct choices	Remarks
Mar. 14	2.230	5	5	
" 14	1.561	5	5	
" 15	1.561	5	5	
" 15	1.301	5	5	
" 15	1.115	10	10	
" 16	1.115	5	5	
" 16	1.041	5	5	
" 16	0.975	10	10	
" 17	1.041	5	5	
" 17	0.975	5	5	
" 17	0.940	10	9	Not punished.
" 18	0.975	5	5	
" 18	0.940	5	5	
" 18	0.867	10	9	
" 19	0.940	5	5	
" 19	0.867	5	4	
" 19	0.822	20	17	Light charge on punishment grills.
" 19	0.781	5	4	Frightened by falling door; refused to work after trial 5.
" 20	2.230	5	5	Refused to work when width of striae was reduced.
" 21	2.230	5	5	
" 21	1.561	5	5	
" 21	0.975	5	5	
" 21	0.867	10	10	
" 22	1.561	5	5	
" 22	0.975	5	4	
" 23	0.975	5	5	
" 23	0.940	5	4	Light charge on grills; not disturbed.
" 23	0.867	10	8	
" 23	0.822	20	15	
" 23	0.940	5	5	
" 24	0.867	5	4	
" 24	0.822	10	9	
" 25	0.940	5	4	
" 25	0.867	5	4	
" 25	0.781	10	8	
" 25	0.743	10	7	
" 26	1.115	10	9	
" 26	0.867	5	5	
" 26	0.781	5	5	
" 26	0.710	10	7	
" 27	1.041	5	5	
" 27	0.822	5	5	
" 27	0 679	10	2	Irregular position choices without hesitation.
" 27	1.041	5	5	Width of 0.710 taken as threshold value; subtends 4′ 4″ of visual arc at distance given—60 cm.

TABLE 4

Record of Chick 2

Date	Width of striae (mm)	Number of trials given	Number of correct choices	Remarks
Dec. 18	2.230	10	4	In general room illumination.
“ 19	2.230	10	4	Very light charge on grills; no disturbance.
“ 20	2.230	10	4	
“ 21	2.230	10	3	Tendency to choose box where last fed.
“ 22	2.230	10	2	Tendency to choose box where last fed.
“ 24	2.230	10	7	Not worked previous day; box being altered.
“ 25	2.230	10	3	Disturbed by punishment.
Jan. 7	2.230	4	1	Greatly disturbed by punishment; removed.
“ 8	2.230	10	6	Very inactive; charge reduced.
“ 9	2.230	10	4	Inactive.
“ 10	2.230	10	7	Under dark-room conditions; not punished; inactive.
“ 11	2.230	10	9	Not punished; this and following series in darkness.
“ 12	2.230	10	9	Not punished; responses slow.
“ 13	2.230	10	9	Not punished; slept 23 minutes; active after trial 3.
“ 14	2.230	10	7	Light charge on grills.
“ 15	2.230	10	5	
“ 16	2.230	10	9	
“ 17	2.230	10	7	Very slow.
“ 18	2.230	10	8	Very slow.
“ 19	2.230	10	9	
“ 20	2.230	10	8	
“ 21	2.230	10	10	Considered ready for stimulus-threshold tests.
“ 22	1.951	10	10	
“ 23	1.951	10	10	
“ 24	1.735	10	10	
“ 25	1.561	10	10	
“ 26	1.419	10	10	
“ 27	1.301	10	10	
“ 28	1.301	10	8	
“ 29	1.301	10	8	
“ 30	1.301	10	10	
“ 31	1.201	10	9	
Feb. 1	1.201	10	8	
“ 1	1.201	10	6	Series delayed about 5 hours.
“ 3	2.230	10	10	Preliminary practice series deemed advisable.
“ 3	1.201	10	10	
“ 4	2.230	10	10	
“ 4	1.115	10	10	
“ 5	2.230	10	9	
“ 5	1.041	10	10	
“ 6	2.230	10	10	
“ 6	0.975	10	10	
“ 7	2.230	10	10	
“ 7	0.940	10	8	Bird in poor condition after prolonged fighting.
“ 8	2.230	10	10	
“ 8	0.867	10	5	Greatly excited by “inductive kick;” see note.
“ 9	2.230	5	4	
“ 9	0.867	10	8	One wing badly lacerated from fighting.
“ 10	2.230	5	5	
“ 10	0.781	10	8	

TABLE 4—*Continued*

Date	Width of striae (mm)	Number of trials given	Number of correct choices	Remarks
Feb. 11	2.230	5	5	
" 11	0.710	10	2	
" 12	0.867	10	10	
" 12	0.743	10	6	This point taken as stimulus-threshold for purposes of succeeding work. Each of the individual striae subtends 4′ 14″ of visual angle at distance given—60 cm.

amenable to statistical treatment. As soon as the problem reaches a certain stage of difficulty, old variable factors, "position-preferences," etc., reappear. It is estimated by students with long experience in this work that the limit of accuracy in determining an animal's threshold is several per cent in either direction. It would appear that such values as are found show the order rather than measure the limit of his ability.

For the sake of those who are especially interested in a comparison of the vision of other animals with human vision under similar conditions I have also used some human observers in this work. It was impracticable at this time to resort to the discrimination method with them, owing to other work which could not conveniently be interrupted. Using the same test field as was used with these animals, under the same conditions of illumination, and at the same distance from the eye, I tested the threshold of five members of this staff by the method of limits with constant change of stimuli. At each observation the test-bands were made quite large and then gradually reduced, the subject being instructed to announce when they became invisible. They were then made still smaller and increased until the subject announced that they were visible. The mean of these two readings was taken as the threshold for that observation. This procedure was repeated ten times for each subject and the mean threshold determined, the mean variation being taken as indicating the reliability of the determinations as the measure of his visual acuity. The subjects are all attached to the research staff of this laboratory, four being physicists and one a physiologist. All are skilled photometrists. Their results are shown below, along with those obtained on J., a high school student.

Subject	Mean Threshold	M. V. %
F	48″	3
Co	50″	3
L	54″	3
Ca	48″	2
W	46″	4
Average	49″	3
J	54″	4

I do not wish to be understood as presenting these results as data fit for strict comparison with the results obtained by the discrimination method. The attitude of the observer is different in the two cases, and the problem is also different. However, we may justly conclude from them that the visual acuity of Monkey 2 is of the same order as that of the well trained human observer under similar stimulus-conditions; while the former showed a visual acuity on the order of four times as great as that shown by the chicks. Closer comparisons are not warranted.

SUMMARY

Definite positive results were not obtained in the tests made on the dog. All his behavior is consistent with the hypothesis that he is insensitive to differences of detail in visual objects. The results are not definite enough to warrant such conclusion, however.

The visual acuity of the monkey compares favorably with that of the human subject under similar conditions.

The visual acuity of the chicks appears to be not over one-fourth that of the monkey under similar conditions.

The dog's behavior demonstrates the necessity of eliminating the possibility of the animal choosing or rejecting an alley on the basis of the presence or absence of electrical charge. The precaution taken in this work is adequate for that purpose.

The present results raise further questions: what are the optimal conditions as to brightness, surroundings, distance of test-fields, range and relative intensities of wave-lengths and adaptation for visual discrimination in these animals, as determined in similar tests ?

PAWLOW'S THEORY OF THE FUNCTION OF THE CENTRAL NERVOUS SYSTEM AND A DIGEST OF SOME OF THE MORE RECENT CONTRIBUTIONS TO THIS SUBJECT FROM PAWLOW'S LABORATORY

SERGIUS MORGULIS

Nearly ten years ago, Professor Pawlow inaugurated the analytical method[1] for the investigation of the function of the nervous system, now widely known as the method of conditioned reflexes. In this short time a mass of material has accumulated which could easily fill a volume and the discoveries made by the numerous workers in that field warrant a thorough revision of our views and teachings regarding the higher functions.

---

[1] It will not be amiss, perhaps, to lay special stress on the strictly analytical character of Pawlow's researches. His point of view is thoroughly materialistic, and his terminology and methodology alike are most consistently objective. The results obtained in his laboratory are, therefore, of extraordinary importance. I am greatly obliged to Professor T. B. Robertson of the University of California, who recently inspected Pawlow's laboratory, for some additional points concerning the experimental procedure adhered to in the conditioned reflex work of which I had no information from reading the literature.

The construction of the laboratory is such that no vibrations of any kind can affect it. The animals, during the experiment, are placed in separate compartments enclosed by walls composed of several layers which make them absolutely vibration-proof and sound-proof. The experimenter is invariably outside the compartment and the entire experiment is conducted by automatic arrangements. The stimuli are produced from the outside and the food is also dropped into a dish in front of the animal from a suspended box which opens and closes by a compressed air apparatus operated by the experimenter.

The salivary flow, recorded in drops, is in reality measured most accurately. This is done by either of two methods. A manometer, several feet long, is connected to a small air chamber into which the saliva flows and the amount is measured by the displacement of the meniscus. The manometer is calibrated with drops of a standard size, causing a displacement so extensive as to enable very precise measurement. The other method consists of an electrical device. The saliva flows through a capillary tube and the drop formed at the outgoing end of the tube, as it falls through a somewhat wider channel, strikes two platinum wires making a contact which is marked on a smoked drum. The time is likewise recorded automatically. In either case the recording apparatus is outside and is inspected without disturbing the animal.

Considering the ideal experimental conditions which are observed by Pawlow and are the direct outcome of his mechanistic-analytical point of view the following statement which he made at a scientific meeting in Moscow and pointed against our students of animal behavior may not seem wholly unjust. He said—"The lion's share of these investigations is at present contributed by the new residence of science—North America. But in these American investigations of the behavior of higher organisms there is still, to my mind, a conspicuous flaw hindering the success of the undertaking which will be unquestionably rectified sooner or later. This is the use of psychological conceptions and classifications in investigations which are truly objective. Hence comes the frequent aimlessness of their complex methods and the invariable lack of cohesion and system in their material which is without a well planned foundation."

It is well known that ordinary spinal reflexes, such as sneezing, coughing, etc., are responses to an external irritation and are characterized by the constancy and certainty of their action. The stimulation starting from a sense organ, or nerve ending, travels to the lower region of the central nervous system, whereupon a reaction is set up by a centrifugal impulse conveyed over the motor nerve. These reflexes are essential to the existence of the organism, they are permanent, inherent and, hence, unconditioned. We know of them only their beginning and end, the action and reaction, but we have no knowledge of the manner in which one is transformed into the other, because we invariably find these reflexes in an already formed condition.

This is quite different in the case of conditioned reflexes. As the name implies, their existence depends upon certain conditions and they appear or disappear under definite circumstances. They arise continually in the nervous system and enter into various temporary associations with other reflexes. In other words, they are exceedingly mobile, uncertain, and temporary in nature. A conditioned reflex is a reaction to an indifferent stimulus, occasioned merely by a repeated coincidence of the latter with a physiologically active stimulus. Its nature is best understood from the manner in which it is ordinarily formed. If a definite sound is produced while the mouth cavity is irritated with acid, and this combination is repeated several times in succession, it will sooner or later happen that the sound will call forth the same reaction which was produced by the acid. The sound has thus assumed a vicarious function and besides affecting the ear, occasions a definite flow of saliva. It has become a stimulus of salivary secretion, and a new salivary reflex is established which, however, is a conditioned reflex, as it is neither permanent nor invariable in its occurrence.

Conditioned reflexes can be formed also with activities other than the salivary secretion, but this has been used almost exclusively by Pawlow and his associates as an indicator of nervous processes. The temporary nature of the conditioned reflexes presents an unusual advantage for the study of the transformation of a centripetal stimulus into a centrifugal impulse.

It has long since been recognized that the central nervous system is a double apparatus consisting of a receptive and an executive portion. Purposely or inadvertently the older physiology overlooked, or at any rate failed to realize, the significance of the interlocking mechanism of both of these apparatus. Yet this intermediary point is of the utmost importance, as it is here that the chief nervous processes take place and all factors acting upon the central nervous system are minutely analyzed. The reflex arch must, therefore, be considered as consisting of three parts: the part which commences at any terminal end of a centripetal nerve and leads to a sensitive cell in the brain, an interlinking piece between this and the third part, which is the executive or effective portion of the reflex arch.

In the study of the physiology of the central nervous system, the first two are of especial significance. From Pawlow's point of view all psychic activity is nothing else than a complex nervous function which is fulfilled by two mechanisms, identified with the first and second portions of the reflex arch. One serves to break up the complexity of the outside factors into their ultimate elements; the other serves to bring various agents of the outside world into temporary association with fundamental organic functions. One is the mechanism of analysers consisting of a receptive organ, its nerve connection and central sensory cell in the brain or cord.[2] The other is the mechanism of conditioned reflexes. The latter has no specialized centre in the cortex such as, for instance, the association centre, but the large hemispheres as a whole must be regarded as the special organ of conditioned reflexes. Conditioned reflexes can be formed provided the cortical portion of the particular analyser is intact. By destroying different sections of the cortex one or another conditioned reflex may likewise be destroyed, leaving the others unaffected, while total extirpation of the hemispheres results in complete abolition of all conditioned reflexes.

---

[2] I take this opportunity to correct a serious error committed in an earlier communication to this Journal. In reviewing the research on auditory conditioned reflexes I have identified Pawlow's analysers with the mechanism of receptors. As will be seen from the above definition the conception of the analyser is more comprehensive and really embraces the idea of a receptor as one of its elements. The receptor is merely a new term for the old sensory organ, whereas the analyser is the receptor plus its special nerve connection and the corresponding sensory cell in the cortex. It is interesting to state that Pawlow distinguishes besides the ordinary visual, auditory, olfactory, etc., analysers, also a locomotor analyser which signalizes into the central nervous system every movement of the muscles and bones. In the text it is related how such purely locomotor sensations can be made the basis of conditioned reflexes, just as stimulation by light, sound, etc.

On the basis of these and many other facts, Pawlow regards the hemispheres the seat of conditioned reflexes just as the spinal cord is the seat of unconditioned, permanent, or inherent reflexes. The large hemispheres, according to this view, are the central station of the various analysers, both external, such as the auditory, visual, etc., and internal, of which the locomotor is the most important.

By means of centripetal nerves from every articular surface, tendons and muscle, each phase of the organism's movement is signalized into the central nervous system where they frequently combine with other organic functions. That this motor analyser with its headquarters in the cortex of the hemispheres is just as real as the tactile, olfactory and other external analysers is demonstrated by the fact that it, too, can form conditioned reflexes. Thus Krasnogorski could establish a salivary reflex to the movement of the knee of the dog's hind leg. Every time the knee was bent a secretion of saliva started in a reflex way. It was a simple matter to prove that the conditioned reflex thus formed was actually associated with an internal motor and not with an external tactile stimulation, as might be supposed. If in a dog with such a reflex to the bending of the leg, the gyrus sigmoidens was excised the reflex immediately vanished, although a salivary response to the stimulation of the skin still persisted. If, on the contrary, the gyri coronarius and ectosylvius were removed, the knee conditioned reflex could be obtained while the tactile reflex completely disappeared.

The all-important fact brought out by the experiments on extirpating certain brain areas, namely, that the hemispheres are the seat for the mechanism of conditioned reflexes and that the destruction of definite regions is accompanied by loss of already established conditioned reflexes or by an inability to form temporary connections with those analysers whose central portion has been impaired—this is the foundation for an entirely novel interpretation of various psychic phenomena. The chief result of its recognition is the substitution of a strictly objective physiological point of view for an indeterminate psychological thinking. The conception of psychic deafness or psychic blindness, for example, which has been developed by Munk on the basis of his extirpation experiments of the occipital and frontal lobes must be discarded as meaningless. Munk's dogs, whose brains were deprived of the visual centre, could neither distinguish one thing from another nor recognize their owner, but they invariably avoided obstacles in their way. The psychological interpretation that animals with such brain defects "can see" but "cannot understand" is no longer necessary. With the destruction of the central and most delicate portion of the visual analyser, its power to differentiate light stimuli is much restricted. Depending upon the degree of injury, the power to analyze the very complex visual factors may be partially or entirely lost. The dog which avoids an obstacle but does not recognize its master has retained the more primitive and more generalized function of the visual analyzer to differentiate between intensities of light but it has lost the *finesse* of the mechanism necessary to differentiate form, color, etc. The study of conditioned salivary reflexes substantiates this view. With a slight injury to the occipital lobe it was possible to form conditioned reflexes to such factors as movement, form, etc. With a more serious encroachment upon the integrity of this portion of the brain the grading between light and shadow alone could be made a conditioned stimulus for the salivary gland.

In this connection it is interesting to review a series of experiments with a dog whose central portion of the tactile analyser has been removed. Prior to the operation on the brain several conditioned reflexes were worked out with this animal to both tactile (thermal and mechanical) and auditory stimuli. The behavior of this operated dog was peculiar in one respect only. When placed anywhere in the room it would remain in the same position indefinitely without ever moving a limb. Its legs seemed to be paralyzed and fastened to the underground, but other parts of the body behaved normally. All conditioned salivary reflexes to irritation of the skin were lost. The lower reflexes of the spinal cord, such, for instance, as the defensive reflex, still persisted and every time the dog was petted, though no ill intentions were revealed, it scowled, barked and attempted to bite. This happened even if food was offered at the same time and is due to the absence of the higher centre of the tactile analyzer. The behavior of the dog among solid objects was very remarkable, because the delicate adjustment of the organism to its environment through its elaborate system of analysers was interrupted at one essential point. The immobility of the dog is apparently of the same origin, as it is believed that the locomotor activity, which is a succession of reflexes, begins with the stimulation of the skin of the soles, which in this specimen is incapable of intermediating between the inner and the outer world of the animal.

The conditioned salivary reflex to auditory stimuli formed before the extirpation of the tactile region in the hemispheres retains its full strength in the operated dog. Furthermore, new conditioned reflexes can be formed after the operation, showing that the function of the central nervous system remains normal wherever the mechanism of stimulation and response is intact; where this mechanism is impaired there is lack of function. To the psychologist this animal with the central part of the tactile analyser missing is a complete enigma. From his angle the animal appears as an irreconcilable contradiction, being abnormal in one environmental relation, and entirely normal in another. But from the objective, analytical point of view, this is very plain, the dog behaving normally where the paths of communication with the outside world are physiologically uninterrupted.

The problem of the localization of functions in special centres of the brain suggests itself here. If an animal with some specific brain defect is observed for a long time it is noticed that the defect wears off in time. Complete recovery probably never occurs, but the disturbed equilibrium with the environment is more or less restored. No matter how seriously the brain has been infringed upon, its integral function returns again. This would indicate that the old idea of the large hemispheres as a unit, superseded in 1870 by the theory of localization, is now to be revived. The investigation of conditioned reflexes brought out very clearly the wide range of substitution occurring in the brain after extirpations. There is as yet no information as to the nature of this substitution, but possibly it is to be traced to the same common cause which underlies the generalization of newly developing conditioned reflexes, as will be shown presently.

We will now examine the various phases in the formation of a conditioned reflex. Any external factor acting upon an analyser may be brought into temporary association with a definite physiological activity as, for instance, the activity of the salivary gland. This association is brought about by repeatedly combining that factor with the physiological stimulus of the gland (food, acid). When after a time such a connection is formed the particular factor which previously had no relation to the salivary gland now affects it as a stimulus. It is very significant that at the moment when this connection first becomes established any stimulus from the same receptive surface acts as a conditioned stimulus of the gland. But as the particular stimulus—smell, sound, light, etc.—is repeatedly applied simultaneously with or in a definite time relation to the feeding, the response of the animal becomes more and more specialized. We distinguish, thus, two phases in the formation of the conditioned reflexes which are so constant as to justify their formulation as two definite laws. The first is the law of radiation of nervous processes in the brain. This may be pictured to one's self so that every stimulus upon reaching a definite sensory cell in the cortex of the hemispheres diffuses over the entire centre. The law of radiation may be demonstrated by an old physiological experiment. If a definite region of the cortex is stimulated a short time, a certain set of muscles is thrown into contraction. If, however, the stimulation continues, it diffuses, radiates over a larger area and at last over the entire cellular mechanism of the cortex, whereby many other groups of muscles become gradually involved in the reaction. The stronger the irritation of any particular point of the cortex the wider it diffuses and the more it subordinates to its influence other less irritated elements. It is interesting to note that in the very extensive experiments on conditioned reflexes it has been discovered that if the desired stimulus is applied about ten seconds before feeding and is continued during the feeding the reflex will be formed after a few trials. If, on the contrary, the dog is first fed, then, ten seconds later, the stimulus is applied as usual, the desired conditioned reflex cannot be established, no matter how often and persistently this combination is tried.

Parallel to radiation an opposite phenomenon invariably occurs, and this is expressed in the second law of the concentration of nervous processes. In this way, by continued repetition, the diffused auditory reflex becomes so differentiated and concentrated that the stimulation of 1,012 vibrations may be received as distinct from that of 1,000 vibrations, or 94 strokes of the metronome as different from 100 strokes.

The gradual concentration of the nervous process with the resulting differentiation of the stimulus is due to the development in the central nervous system of inhibitory processes. This can be demonstrated by numerous facts. If a conditioned reflex has been worked out to a sound of 1,000 vibrations with such precision that 1,012 vibrations are differentiated into a distinct stimulus the following interesting things can be observed. Whenever the sound of 1,000 vibrations is produced, a definite quantity of saliva is secreted; whenever the 1,012 vibrations are tried no salivary reflex is obtained. If, however, the effective stimulus is applied immediately after the ineffective, it is found to have either no influence or only a very feeble influence on the salivary secretion. Its original effect as a conditioned stimulus of the salivary gland is regained only after considerable time. It is obvious, therefore, that the differentiated stimulus caused an inhibition, and in virtue of this inhibitory action of unusual stimuli the sphere of influence of the usual stimulus becomes gradually restricted until at last it travels over a completely isolated path in the cortical portion of the analyser.

This hypothesis of differentiation as the result of inhibition is supported by several considerations. In the first place it is possible to offset an accomplished differentiation by reactivating those portions of the cortex whose susceptibility for the differentiated stimulus has been checked. This is, indeed, a common experience and can be demonstrated by a simple experiment. Here is a dog with an auditory conditioned reflex differentiated to one-eighth of a tone. The differentiation is so sharp that in no instance will a sound one-eighth of a tone different from the familiar one stimulate the secretion of a single drop of saliva. If, however, some unusual noise should be made during the experiment which excites the animal the differentiation of the auditory conditioned reflex will be temporarily lost and the salivary reflex will occur in response to any tone. This state of affairs may last fifteen to thirty minutes, when the differentiation becomes once more very rigid.

The hypothesis receives further proof from the fact that the inhibition can be increased by repeating the differentiated stimulus several times. In other words, the inhibition is cumulative. Suppose the dog reacts to a familiar sound with a secretion of nine—ten drops of saliva. A differentiated tone calls forth no secretion, while the familiar sound produced immediately afterwards causes this time a flow of seven—eight drops of saliva. The experiment is then repeated with a modification, the differentiated tone being now produced three times in succession. The familiar sound is again applied, but this time its influence is still more suppressed and only three—four drops of saliva are obtained.

Lastly, if differentiation is the result of inhibition, it is to be expected that the finer the degree of differentiation attained the greater would be the inhibition. The evidence in this respect is also very favorable. If an auditory conditioned stimulus is applied, then a sound one-eighth of a tone higher, the repetition of the former, familiar stimulus exerts no influence on the salivary gland. If, however, a sound one or several tones different is employed, the conditioned salivary reflex to the familiar sound remains now unaffected. This points very clearly to the conclusion that the finer the differentiation the more intense the inhibition.

It is a natural expectation that the inhibition or suppression arises within the corresponding analyser. This can be shown to be true by means of an experiment. If in the previous experiment with the auditory conditioned reflex the familiar sound had been associated with irrelevant stimuli of various kinds, it would have been invariably found that neither visual nor olfactory nor any kind of stimulus except auditory left an imprint upon the conditioned reflex, showing that the inhibitory processes developed in that analyser.

The higher nervous processes are not stable but dynamic, constantly changing, overflowing large territories in the nervous system, then concentrating into narrow channels again. The laws of radiation and concentration are even more strikingly shown in the matter of inhibition. Starting in some one particular analyser the inhibitory process may radiate towards other centres in the large hemispheres. The diffusion of the inhibitory wave is apparent where the inhibitory process is experimentally cumulated. Two conditioned reflexes, visual and auditory, may be worked out in a dog. The introduction of a differentiated auditory stimulus suppresses the action of the established auditory conditioned reflex, but the visual reflex is free from any trace of inhibition. The differentiated auditory tone is now repeated several times in succession, in which case not only the auditory but the visual reflex likewise shows unmistakable signs of inhibition. The inhibition starting in the auditory centre radiated beyond its limits and penetrated into other centres in the cortex.

Here is another very remarkable example. A series of five scratchers are arranged along the hind leg of the dog which irritate the skin mechanically in certain places. The four upper instruments are always used while the animal is being fed, and the irritation of those four spots is a conditioned stimulus of the salivary gland. The fifth scratcher is ineffective owing to the circumstance that its action on the skin has never been accompanied by an unconditioned stimulus. But if it is employed once, the four others above it lose their influence for a certain length of time and it is possible to observe how rapidly the inhibition spreads to neighboring points in the same centre of the large hemispheres. The more, however, the interval between the action of the fifth and of the other four scratchers is prolonged, the more are the latter freed from the influence of the inhibition wave which gradually recedes to its point of origin. Repeating the same experiment several times, the period of recession of the inhibition wave becomes continually shorter until an inhibitory action is hardly perceptible.

Corresponding to the very complex relationship between the ever-changing environment and the organism, adapting itself by means of conditioned reflexes, several forms of inhibition have been recognized and described. Sleep is one form of inhibition splitting as it were the existence of the organism into an active and passive phase and either diminishing or completely obliterating all conditioned reflexes. Another important form of inhibition is the external inhibitory process which results from the competition between stimuli affecting the cortex. Every new factor comes in collision with others already acting in the brain and either draws to itself the available supply of energy or is crowded out by the more intense stimuli. In general terms it means that a strongly irritated point in the central nervous system lowers the affectibility of adjacent regions. There is still a third form of inhibition characterized as internal inhibition.

This is a phenomenon of rapid but only temporary paralysis of conditioned reflexes occurring whenever conditional stimuli do not truly and precisely inform the central nervous system of unconditioned stimuli, in other words when the conditioned stimulus is not reinforced by the physiological irritation which accompanied its formation.

There are several kinds of internal inhibition. Waning conditioned reflexes, due to a repeated application of the conditioned salivary stimulus without the aid of an unconditioned stimulus, is one kind. Another kind is the delayed reflex which appears if the conditioned stimuli are regularly followed by feeding a few seconds or even minutes after the conditioned stimulation has ceased. Conditioned inhibition is likewise a form of internal inhibition arising when an irrelevant factor is added to the conditioned stimulus, the combination not being reinforced by feeding. In such a combination the conditioned stimulus is quite ineffective, but alone it exerts the usual influence. The process of differentiation and concentration, already described above, represents a still other type of internal inhibition—the inhibition of differentiation. Furthermore, it is a very common and very important occurrence that an inhibition checks another inhibition, the result being a reactivation[3] of the inhibited reflex.

It is quite evident from what has been said that inhibition is an active process in the nervous system fully comparable to the process of irritation. The results of all investigations point strongly to the conclusion that the process of internal inhibition is much less stable than the process of conditioned stimulation and can be offset by the least outside disturbance.

Recently a new type of conditioned reflex has been discovered, the so-called secondary conditioned reflex. If a perfect conditioned reflex to light has been worked out in a dog and a definite sound is now added to it a few times in succession, while this combination of the familiar light and unfamiliar sound remains unsupported by the physiological stimulus, it has been observed that the sound without the light causes a salivary reflex. This secondary reflex is usually of very feeble action, causing the secretion of one or two drops of saliva, and vanishes very quickly.

---

[3] The Russian term applied to this phenomenon has no appropriate English equivalent. The German " Loshemmung bedingter Reflexe " is a literal translation.

This very interesting question of the secondary conditioned reflexes is, however, still in the initial stages of investigation.

Thus from the objective, physiological point of view " this seemingly chaotic and infinitely complex, ever-changing reaction of the organism to the flux of countless influences of the outer world, in a word, all that is commonly called psychic activity, is nothing but an endless chain of reflexes, i.e., determined responses to the environment. The kaleidoscope of conditioned reflexes in its fantastic and apparently irregular and undefinable play in reality is controlled by rigid laws, by the intensity, duration and direction of the nervous processes in the large hemispheres."

In the foregoing two remarkable facts have been mentioned in passing, the further discussion of which has been purposely deferred until this moment. It will be recalled that a noise produced during an experiment, which excited the animal, caused simultaneously the disappearance of a previously established differentiation. If the dog could recognize one-eighth of a tone it would now, under the excitement, give the conditioned salivary reflex to any sort of auditory stimulus. Psychologically speaking, the animal was in a state of affectation. Physiologically, the strong irritation radiated over a large territory in the brain and so affected the tonus of its nervous elements that all signs of inhibition were temporarily masked.

It will further be recalled that the experience of workers in this subject is that no matter how persistently one may try it is impossible to work out a conditioned reflex to any factor whatsoever if the physiological stimulus (food) is employed before the stimulus, which it is desired to make a conditioned stimulus, is used. On the contrary, if such a stimulus is followed up by the physiological stimulation a salivary reflex is created very speedily. To understand this fact it must be regarded in the light of the general statement—as given above—that a heightened state of irritability in one part of the cortex lowers the susceptibility of adjacent parts, and that the stronger the irritability the wider the range of its influence.

Here are a few other similar instances. A watch dog of a highly nervous temperament with a well formed conditioned reflex is the subject of an experiment, which is to be conducted by a stranger. The appearance of this stranger in the laboratory, especially if his manner is at all provocative, causes a furious outburst of an aggressive reaction on the part of the dog. The stranger proceeds with the experiment in spite of the dog's excitement, applies the familiar conditioned stimulus, and to the general astonishment, gets an unparalleled response from the salivary gland. If he continues the experiment longer and the dog gradually becomes quiet the conditioned salivary reflex commences to fade and at last the secretion ceases. The least movement on the part of the stranger will at once rouse the dog's fury and immediately thereupon the conditioned salivary reflex will wax strong again and the story will repeat itself.

This experiment has wide theoretical bearings, revealing clearly the interaction of different centres of activity in the hemispheres. An intense irritation of the aggressive centre radiates out from the point of origin and invades the other centres in the brain, causing a general increase of the nervous tonus of the cortex. This involves also the secretory centre. But as the tide of excitement recedes to the aggressive centre the above formulated law of competition of co-existing factors comes into prominence, an external inhibitory process sets in and as a result of that the action of the salivary centre is suppressed.

Here is still another very striking case. The skin of a dog is irritated by an electric current of such strength as to cause a painful sensation (or a destructive action, in accordance with the objective terminology). Each time this stimulus is applied the mechanism of self-defense is set into a vigorous reaction; the animal attempts to break loose from the stand, to snatch the instrument, and so on, in other words, a strong defensive reflex results. If food is given to the dog at the same time (this must frequently be done through a stomach tube) it sooner or later comes about that the defensive reaction is gradually subdued and at last vanishes altogether, while the electrical irritation becomes a conditioned stimulus of the salivary gland. Two important things must be considered in this connection. First, the blocking of the irritation of one centre (defensive) by the activity of another (nutritive) and, secondly, the diversion of the stimulus into a new channel towards a point in the cortex of more intense function. The nutritive centre[4] which is physiologically very important, draws to itself the available nervous energy, leaving thereby other centres ineffective. The force of this interpretation is easily recognized by a modification of the above experiment. If, instead of food, an acid is used in stimulating the salivary gland—the acid likewise being an unconditioned stimulus of salivary secretion, but one which is ordinarily rejected by the animal—the painful sensation of the electric current can not be overcome nor can a conditioned salivary reflex be developed under these circumstances.

---

[4] Pawlow is of the opinion that the animal possesses a nutritive centre which resembles in every essential the respiratory centre. It is beyond the limits of this article to discuss this point further. I wish to make, however, this comment upon

Many seemingly miraculous events of human experience become intelligible in the light of these experiments. The mutilation of the body practiced by certain sects in an ecstasy of religious fervour, the apparent insensitiveness to excruciating pain demonstrated by many martyrs of a creed or ideal, absolute disregard of fatal injuries when the nervous energy is mustered in a life or death struggle—these and many others are phenomena obeying definite physiological laws.

If we reflect upon what has been said and fix our attention on the thing which is common to all these diverse facts the conclusion will not be unwarranted that the function of the higher centres of the brain is governed by a fundamental principle of the flow of nervous energy towards points of the highest irritation.

Consciousness and unconsciousness, according to Pawlow, are purely physiological phenomena of the same order. Consciousness is a state of a part of the large hemispheres characterized by an optimum affectibility. At a given time and under given circumstances new conditioned reflexes and differentiation of conditioned stimuli develop here rapidly. This is, therefore, the creative centre of the hemispheres at the particular moment. All other parts of the hemispheres are in state of diminished affectibility. Only stereotyped, long established conditioned reflexes are displayed there at that moment; they are the seat of unconscious processes. The distribution of parts of optimum and minimum susceptibility in the hemispheres is not fixed;

Pawlow's frequent use of the term "centre." Nowhere, so far as I know, does he commit himself definitely to the question of localization of centres in the brain. It is clear none the less that he assumes localization only in the broadest sense. Centres are to him physiological entities rather than anatomically distinct areas. Since every point of an analyser has a corresponding cell in the cortex, the impulses from a certain analyser naturally travel to a definite region in the hemispheres. But there is also much interlocking between adjacent centres which seem to wedge into each other. Besides, the cortical elements seem to be functionally interchangeable, at any rate his extirpation experiments bear out such a conclusion.

the brain is essentially dynamic, its elements constantly throb with activity, and now one, now another dominates over the higher functions.

In concluding this section of the paper I cannot forego to quote the following picturesque sentence of Pawlow: "If it were possible to look through the skull and if the region in the hemisphere of optimum affectibility were lighted up, we might see in the thinking conscious human being a bright spot of fantastically ragged outline, of perpetually changing form and size and migrating over the hemispheres surrounded by more or less complete darkness hanging over the rest of the hemispheres."

FRIDEMAN, S. S.—Further Contributions to the Physiology of Differentiation of External Stimuli.

The object of this investigation was to find out where the differentiation of an auditory conditioned stimulus takes place: in the auditory analyser or in that cortical portion of the nutritive center upon which the corresponding unconditioned stimulus acted. The procedure was this: a conditioned reflex to a sound of 2,600 vibrations per second was worked out on the basis of direct salivary stimulation with meat-powder, and the stimulus was differentiated for a tone of 2,324 vibrations. Then a conditioned reflex to the higher tone was worked out with the aid of acid irritation and the differentiated tone tested again. If the differentiation still exists—as it was actually found to be the case—it means that the specialization occurs in the auditory centre. The author further found that it is easy to establish a conditioned reflex on the basis of the meat powder after such has been established to acid, but not *vice versa*.

TCHECOTAREVA, O. M.—Further Contributions to the Physiology of Conditioned Inhibition.

The conditioned inhibition is proven to be a form of internal inhibition. The effect of this inhibition is subject to summation by repetition. By persistently testing the reflex after the inhibition the reflex may be released of its influence. Irrelevant stimuli, especially of the same analyser, destroy the inhibitory action. The process of conditioned inhibition remains potent even after some conditioned reflexes have been freed of its influence.

THEOCRITOVA, U. P.—Time as a Conditioned Stimulus of the Salivary Gland.

By stimulating the gland with food at strictly regular intervals a specific salivary reaction may be formed on a time basis. The conditioned reflex thus established resembles exactly other conditioned reflexes. It is not very stable, however, and wanes after the first failure of reinforcement by the unconditioned stimulus. The nervous system is capable of very minute differentiation of time, and the 29th minute is clearly distinguished from the 30th in a thirty-minute period. The specific stimulus of the salivary centre is the functional trace, or after effect, from the preceding stimulation of the food.

VASSILJEV, P. N.—Differentiation of Thermal Stimuli by the Dog.

Warming a circumscribed region of the body to 47° C. has been made a conditioned stimulus. Cooling to 0.2° C. was likewise tried. It is easy to get conditioned reflexes to either of these stimuli, but the two together do not produce two distinct reactions. For a long time they are received as a single stimulus and only by long continued tests may the differentiation be achieved. This suggests close intimacy of " cold " and " heat " centres in that the component nerve cells are not grouped to form separate centres but are interspersed. This explains the generalized character of heat or cold stimulation.

FOLBORT, G. V.—Inhibitory Conditioned Reflexes.

A conditioned inhibitory reflex has been established in the ordinary way by combining repeatedly an inactive stimulus with the natural inhibition of conditioned reflexes. After a while such neutral stimuli become active inhibitory agents. This fact is of much theoretical importance as it shows that a factor acting upon the nervous system is stamped by the prevailing process: it becomes a conditioned inhibition, if it happens to coincide with the inhibitory function; or it becomes a secondary conditioned reflex if it coincides with another phase. Author concludes that the waning of conditioned reflexes is an active process similar to the conditioned inhibitory process.

The indifferent factor, by coinciding with a conditioned reflex which is in a phase of decline owing to intrusive relations, acquires an inhibitory rôle over all conditioned reflexes.

ROJANSKI, N. A.—Materials to the Physiology of Sleep.

Former investigations of this subject are defective because they deal usually not with normal but induced sleep and sleep-like conditions, and besides do not clearly differentiate the question of the periodicity of sleep or the mechanism of falling asleep and awakening. The author studied last phase of the problem with the aid of method of conditioned reflexes. From the objective point of view, the nature of nervous processes during sleep as they are revealed in the muscular relaxation and reaction to the outside influences must form basis of definition of sleep. As an objective indicator of sleep the relaxation of the eye and neck muscles and the cessation of all conditioned reflexes have been used. The depth of sleep is measured by the degree of muscular relaxation which is determined by an instrument devised by the author. The disappearance of the conditioned reflexes is ascribed to the development of inhibition. Mechanical interference with bodily movements acts as a hypnotic influence, and it is believed that spontaneous sleep likewise has its origin in the inhibition of movement. Correspondingly stimuli affecting the muscular system are most potent in disturbing sleep. Conditioned muscular reflexes are, therefore, more effective than the conditioned salivary reflex. Stimuli originating in the urinary bladder or in the thick intestine, both of which are associated with the motor system, are very effective agents in disturbing sleep. The principal source of inhibition is in the motor analyser and spreads secondarily by radiation to other parts of the central nervous system.

The question of the periodicity of sleep must still remain open. It probably depends upon some unknown organic function which periodically favors the radiation of inhibition.

Unconditioned reflexes during sleep increase in strength at first, then diminish below the normal level to increase again just before awaking. Conditioned reflexes wane very rapidly at the beginning of sleep and gradually increase about the time of waking. The physiological source of sleep is the inhibiting developing within the motor analyser. Spontaneous sleep occurs when such an internal inhibitory process is favored by mechanical resistance to motor impulses. The environment, in that event, acts as a sum of brakes. By removing parts of that environment it is possible to offset partially this inhibitory influence.

Active animals employed for the conditioned reflex studies were strapped to the stand so that they could not move a limb. The primary object was thus achieved, the animal having become absolutely quiet, but it is useless for the experiment as it soon falls asleep in this environment. The environment becomes a conditioned inhibition. Every time the dog is placed in the stand and strapped the established conditioned reflexes fail to appear. The effect of the environmental gradient is clearly shown by the following experiment.

Time	Stimulus	Salivary response in drops	Duration of stimulus	Environment
3:50	Metronome	...	30″	Strapped to the stand.
4:00	"	2	30″	Same stand; no straps.
4:12	"	4	30″	Different stand.
4:25	"	7	30″	On the floor.
4:35	"	3	30″	Unfamiliar stand.
4:47	"	0	30″	Usual stand; no straps.
4:56	"	0	30″	Same, strapped.

Savitch, A. A.—New Materials for the Study of the Influence of Nutritive Reflexes Upon Each Other.

The influence of various substances used as nutriment is studied by the method of conditioned reflexes, the organism being either surfeited with or deprived of the particular substance. Meat powder, granulated sugar and cracker meal are used. Two dogs were deprived of meat, being abundantly fed on sugar. The conditioned reflex worked out for the meat powder diminishes very much at first showing thus an intense excitation of the sugar subcentre and an inhibition of the meat subcentre. The overexcitation of the sugar subcentre results, however, in fatigue, whereupon the meat conditioned reflexes increase again. It must, therefore, be considered as proven that food stuffs exert an influence in the direction of inhibition conditioned reflexes established to other food stuffs. But the influence depends upon the organic need of the animal for one or another nutritive constituent, or, in subjective terms, upon its taste. An increased need of the animal of food constituents of which it has been deprived lasts a variable time depending upon the length of privation, and can be easily detected by the degree of conditioned salivary response. The physiological reaction produced by the food materials on the lining of the mouth and on the taste and organs are discerned by the mouth analyser exactly as sound stimuli of different frequency of vibration are discerned by the auditory analyser.

Jerofeeva, M. N.—Electrical Irritation of the Skin of the Dog as a Conditioned Stimulus of Secretion of the Salivary Glands.

The irritation caused by a sharp instrument inhibits both the natural and artificial conditioned salivary reflexes. The degree of inhibition depends upon the strength of the irritation. The inhibition caused by irritation with the sharp instrument gradually decreases, i. e., this irritation represents a waning inhibitor. A weak faradic current has a similar effect and may become the conditioned stimulus of secretion. The faradic current of such slight strength may, however, cause also a sleeping reflex. The sleepy state induced by the electric current is not as deep as when produced by a thermal stimulus. The sleeping reflex occasioned by the electrical stimulation is accompanied by salivary secretion in response to various irrelevant factors. During sleep the conditioned reflex to the electrical irritation as well as to stimulation of other analysis disappears. The sleeping reflex may be counteracted by intermissions in the experiment, by change of strength of current or by change of place of stimulation. This sleeping reflex interferes with the development of differentiation as to the locality of the skin. The conditioned reflex obtained with a faradic current applied to different regions of the body varies in intensity according to the sensitiveness of the skin in the particular region. The least sensitive part of the skin is that directly above spinal column and on top of head. The most sensitive part is on the inner surface of hind legs, on the intercostal spaces and tail.

The irritation of the skin with a very strong faradic current forms a conditioned salivary reflex. As the irritation grows the reflex also increases. The defensive reflex at first called forth by the electrical stimulation is lost when the conditioned salivary reflex appears. Even before the salivary reflex has been fully formed the process of eating soothes the violent defensive reflex. Neither in the case of the strong nor of the weak faradic current can a conditioned salivary reflex develop with regard to acid. 0.25% of HCl, when poured into the mouth apparently blocks the conditioned salivary reflex to electrical stimulation, while it may increase the reflex to an auditory stimulus. The conditioned salivary reflex to the stimulation with an electric bell is from the start more intense than to the irritation with a faradic current, and can completely replace the latter. A differentiation of the strength of the electric current can not be accomplished, although the dogs form readily a differentiation with regard to other stimuli. Dogs with a conditioned reflex already worked out on the basis of electric irritation develop without any difficulty or delay similar reflexes to other destructive factors (singing, squeezing, pricking) whereby the defensive reflex never occurs.

NOTES

THE INFLUENCE OF WHITE AND BLACK WALLS ON THE DIRECTION OF LOCOMOTION OF THE STARFISH [1]

R. P. COWLES

(From the Zoological Laboratory, University of the Philippines)

It has long been known that the starfish has at the end of each arm a little patch of pigment. This is generally spoken of as the "eyespot" and is considered to be an organ which is sensitive to light, making it possible for the starfish to react to light of different intensities. For example, it has been shown that certain species of starfishes when placed in a box into which light shines at one end only, will almost invariably move toward that end. In this reaction it is probable that the eye-spots are stimulated by the bright light coming from the open end of the box, but it is also true as I have shown (1909)[2] that when the tips of the arms, including the eye-spots, are cut off and the specimen is kept for several days until it has recovered to some extent from the shock, the starfish will still move, though more slowly and hesitatingly, toward the lighted end of the box.[3] This may indicate that the eye-spots aid in directing the movements of the creature, but it also shows that the general surface of the body is sensitive to light. When a very small spot of light is cast upon the upper or lower surface of the starfish,[4] it becomes evident that the integument or the branchiae, and the tube-feet are very sensitive to changes of light intensity. This is further shown by the fact that a small patch of shadow cast upon the

---

[1] The writer is indebted to Professor E. A. Andrews, in charge of the marine laboratory of Johns Hopkins University at Montego Bay, Jamaica, for the privilege of doing this work.

[2] Year Book of the Carnegie Institution of Washington, No. 8, 1909.

[3] Mangold in a paper which appeared in the same year and possibly before mine found that when the eye-spots were removed from a star-fish the latter still reacted to light.

[4] The light rays were allowed to pass through several centimeters of water in order to reduce the heat factor to a minimum.

surface of the starfish causes the branchiae to contract. It will be seen from these experiments and those made by other investigators that at least most of the surface of some starfishes is sensitive to change in the intensity of light, provided the change is great enough.

The work of Jennings (1907) and Bohn (1908) seems to show that certain species of starfishes which react negatively to light of ordinary intensity often tend, when placed in the sunlight, to move toward opaque walls when these are not too far away. This occurs even when these walls are arranged so that they cast no shadow. Jennings has found that the reaction is quite variable, fully half of the individuals used moving without any reference to the opaque wall. However, in some cases the reaction was so constant that he considered it not to be accidental and he raises the question "as to whether there exists in the starfish anything resembling what we speak of as image formation; resulting in the perception of objects, or at least in a reaction toward objects as such."

The writer has devised a series of experiments in which the object has been to test the behavior of the starfish with reference to white and black walls, keeping other factors which might affect the behavior under control as much as possible.

The apparatus used consisted of a wooden box, 91.5 cm. high, 61 cm. wide and 30.5 cm. deep, set on a cement floor so that the bottom would be level. It was open at the upper end and was painted dull black inside. A rectangular glass dish, 30.5 cm. long, 15.3 cm. high and 15.3 cm. wide, covered with dull black paper except on one side where white bristol board was placed, served as an experimenting dish. The open top of the box was provided with a removable cover of thick broadcloth in the center of which was a hole. Into this hole was fixed an acetylene bull's-eye lamp, so that when the latter was lighted the rays were directed downward into the box. The experimenting dish was so placed in the bottom of the box that its center came directly below the center of the source of light, thus lighting the bottom of the dish without casting any shadows. This apparatus, which to be sure was rather crude in construction, was the best that could be devised in Montego Bay, Jamaica, where the experiments were performed. The constant results, however, obtained with forty individuals of the starfish *Echin-*

aster spinosus indicate that the factors affecting the behavior were well under control.

The method of making a test was as follows: The experimenting dish was almost filled with sea water and set as described above in the bottom of the box; a starfish which had been kept in darkness was placed directly in the center of the bottom of the dish so that the tip of one of its rays was about 2.5 cm. from the white wall; the cloth cover with the light coming through its center was then quickly fastened over the top and the starfish allowed to move. After about 20 seconds, a time sufficient for the reaction to take place, the cover was removed, the position of the specimen noted, and the starfish then put back in a dark receptacle. The method of handling the specimen, the position of the white wall with reference to any possible tilting of the bottom of the dish, the opening and closing of the cloth cover, the position of the arms and madreporite of the starfish with reference to the white wall, were all varied in the tests so as to eliminate any of these factors in the determination of the direction of movement.

Echinaster spinosus, unlike the species used by Jennings, tends to move toward the regions of ordinary light intensity and away from darkness. In 200 tests made with 40 specimens of this species, only in 10 cases was it found that the starfish had moved toward a black wall and in these cases it seemed probable from the position of the specimen that it had not moved there directly. This surprisingly uniform reaction was due to the influence of either the white or the black wall.

What is to be inferred from this behavior ? Does it mean that the starfish has vision ? It seems to me that the behavior is due to the relative illumination of the different parts of the body just as in the case of a starfish moving toward a bright source of light. While in the experiments the lamp was so placed that the walls did not cast what we call shadows, yet those parts of the surface of the starfish near the white wall undoubtedly were more brilliantly illuminated than those near the black wall.

JOURNAL OF ANIMAL BEHAVIOR

Vol. 4 NOVEMBER-DECEMBER, 1914 No. 6

LITERATURE FOR 1913 ON THE BEHAVIOR OF THE LOWER INVERTEBRATES

S. J. HOLMES

University of California, Berkeley, California

In continuing his studies on the rheotaxis of isopods Allee (1, 2) has found that when the positive rheotaxis of Asellus is strong there is a high degree of efficiency in the reactions to the current. Low efficiency is correlated with indefinite or negative responses. When molting occurs sensitiveness to currents is greatly reduced. Low oxygen content and KCN cause a reduction or reversal of the usual reactions. There is little relation between the vigor of the reaction to mechanical shocks and the sign of the rheotactic response. KCN, and lack of oxygen produce at first an increase of sensitiveness to shocks followed by a period of dulled sensitivity. Often sensitiveness is increased during the molting period. No daily rhythms of behavior were observed.

In a series of experiments on the taste and smell of the crustacean Palaemon, Balss (3) concludes that the olfactory sense is located partly in the antennae and partly in other parts of the body. Taste is located not in the antennae, but in the mouth parts and tips of the thoracic legs.

The extensive studies of Bancroft (4) on the much discussed subject of the phototaxis of Euglena have shed much light on several of the vexed questions involved. Orientation which has been considered a function of differential sensibility is found to stand in no necessary relation to the latter. Positive reactions

" may be accompanied by motor reactions to either sudden shading or sudden illumination," and " the ability to react to sudden changes in illumination by means of motor reactions is possessed by Euglenae which are not heliotropic. Conversely, there are heliotropic Euglenae that cannot be made to respond to changes in illumination." The orientation to light and the ability to react to sudden changes of light intensity being to a large extent independent variables, it is concluded that the two types of reaction depend upon different mechanisms. Orientation is not the outcome of trial and error, but " is as direct as the locomotor mechanism of the organism will allow."

Baunacke (5) gives a general discussion of the function of the statocyst in various invertebrates and describes several experiments showing the relation of the statocysts to the preservation of the normal position in various mollusks.

Bohn (6) has given a discussion of modifiability of behavior in lower organisms and its relation to certain physical and chemical processes. That he is correct in ascribing associative memory to protozoans and coelenterates may be questioned by many comparative psychologists, but all will find his treatment of the topic suggestive.

The experiments of Miss Brundin (7) on some terrestrial amphipods from California showed that the more terrestrial of the two species studied, *Orchestia pugettensis*, is the more strongly positive to light. This species commonly lives in holes in the sand above high tide mark, while *Orchestia traskiana* lives in cooler and moister conditions under sea weeds and rubbish nearer the water's edge. It was found that both dryness and heat tend to make negative Orchestias positive. Enforced activity also produces the same effect. Orchestias compelled to lie on one side by being compressed between two glass plates would nevertheless manage to go toward the light. Specimens with one eye blackened over would at first perform circus movements toward the normal side, but after a time they would go to the light in a more direct course. There is a discussion of the relation of the behavior of the two species to the choice of their respective habitats.

Brunelli (8) has given a resumé of the behavior of hermit crabs and adds a detailed description of how *Pagurus arrosor* detaches the anemone *Adamsia* and then places it, base downward, on the shell which this crab inhabits. The author discusses the origin and significance of the symbiotic relations of these two forms.

Buddenrock (9) finds that in Branchiomma and certain other annelids that bore into the mud or sand, the statocyst does not serve for the perception of jars, but affords stimuli causing the side of the tail end in contact with the substratum to bend downward; *i.e.*, the statocyst is the organ of geotaxis. Extirpation of both statocysts destroys the power of boring straight into the earth.

Car (10) gives a not very illuminating discussion of ciliary movement in general and the locomotion of the ciliate infusoria; he also touches upon the movements of gregarines.

After section of the ventral cord of diplopods, Clement (11) finds that co-ordinated movements between the appendages in front of and behind the incision continue to occur. Stimuli afforded by muscular strains are probably instrumental in effecting this co-ordination. Reactions of particular appendages were studied and their influence on the movements of other appendages. Rolling into a spiral, which persists after decapitation, no longer occurs if the first three metameres are removed.

Cole (12) finds that the starfish *Asterias forbesi* locomotes most frequently with the madrepore or one of the adjacent rays in front. This " physiological anterior " of the starfish " corresponds to the anterior of the spatangoids with respect to the position of the madreporite." Starfishes tend to crawl in the same general direction in successive trials, but when changes of direction occur there is a tendency for the locomotor impulse to " shift or rotate gradually around the body in one direction or the other."

In experiments on co-ordination and righting in the starfish, Cole (13) found that individuals with the radial nerves cut near the circum-oral nerve ring were nevertheless able to right themselves. The operation was accomplished only with difficulty owing to the lack of co-ordinated activity in the different arms. Specimens with one or more arms amputated were found to right themselves as were also the individual arms.

Cowles (14) describes the method by which *Cryptodromia tuberculata* St., a sponge-carrying crab, snips loose a piece of sponge, pushes its body under it and carries it off while holding it with the posterior pair of legs. *Alpheus pachychirus* St. has the curious habit of forming a tube of an alga which grows in the form of a sheet of threads. The Alpheus lies on its back, draws the folds of the alga together on either side, then, by pulling the threads through holes made by its feet, actually sews together the folds of the alga to form a complete tube.

By throwing light from various differently colored surfaces on the daphnid Simocephalus, Erhard (16) noted that the eye reacted in the same way as to changes in the intensity of any one color. He concludes, like Hess, that daphnids are color blind.

The behavior of the parasitic copepod *Lernaeopoda edwardsii* has been studied by Fasten (17) who finds that the free swimming young habitually move in a spiral course, thus increasing their opportunities of coming into contact with their host. The larvae are positive even in strong light and swim near the surface during the day, but sink toward the bottom at night. Observations were made on thigmotaxis, geotaxis, reactions to temperature changes, and to various chemicals, and also on the method by which the larvae attach themselves to the gills of their host, the trout.

According to Franz (18) phototaxis is either a device for scattering the species, as when it occurs in the larvae of animals inhabiting the bottom of waters, or in a movement of flight (Fluchtbewegung) by which the animal escapes unfavorable or threatening conditions. For the arguments supporting this unique standpoint reference must be made to the original paper. Franz (19) has also given a more or less popular account of the behavior of snails.

Frisch and Kupelweiser (20), from a series of experiments on Daphnia and Artemia, conclude that these animals have the power of distinguishing different colors. If Daphnias which have become indifferent to a certain intensity of light are exposed to a light of less intensity they become positive, whereas if the intensity of light is increased they become negative. However, if one interposes a blue screen, the daphnids in spite of the diminution of light intensity become negative. If one adds yellow light to the white light to which Daphnids have become indifferent there is evoked a positive reaction notwithstanding the fact that the intensity of the light is increased. Artemia reacts in much the same way as Daphnia, and the author concludes that lights of different wave lengths produce different effects.

Frölich (21) has experimented on the isolated eyes of Octopus, noting fluctuations in the current of action under constant stimulation by light. Rhythmical fluctuations of the current were noted which varied in frequency and extent with the intensity and wave length of light.

Gee (22) has made a thorough investigation of the behavior of two species of leeches, *Dina microstoma* Moore and *Glossiphonia stagnalis* L. His paper includes a description of the general habits of the two species; their various movements; food and feeding; reactions to light, heat, currents of water, and chemicals; daily changes of behavior; the behavior of the young, and various other features of the normal activities of these animals, thus affording a foundation for the analytical work which follows. Under the head of modifiability of behavior are treated the various responses of the animal to repetitions of the same stimulus and their different determining factors, acclimatization to stimuli, fatigue, depression induced by various chemicals and its relation to fatigue, and the influence of hunger and satiety on various reactions. Of particular interest is the parallelism between the effects of fatigue and influence of those substances, sarco-lactic acid, carbon dioxide, etc., which are supposed to cause fatigue in higher forms.

Gee's paper (23) on the modifiability of behavior in the sea anemone Cribrina embodies an attempt to account for the changes of behavior in this form in terms of certain physiological processes. Food produces a copious secretion of mucus and after a certain amount of food has been taken in the animal refuses to take more. Why does the surfeited anemone reject the food ? It is not due to fatigue of the muscles involved in prehension or swallowing. If the anemones are stimulated by beef extract or oyster juice they secrete mucus copiously and soon reject solid food. Various salts were found to cause the anemone to reject food. The refusal of food is not the result of conditions of assimilation; apparently it is the effect of conditions brought about by the secretion of mucus. Cribrina remains expanded in the light and contracted in the dark, and shows no diurnal or tidal rhythms independently of the changes of the stimuli directly affecting it.

In the course of an investigation of the alleged color sense of the lower animals Hess (24) has experimented on various fishes, the larvae of Culex, and the anemones Cerianthus and Bunodes. The general results are confirmatory of his contention that the lower animals are color blind, *i.e.*, they are affected only by the intensity and direction of the light rays.

In the course of a general account of the biology of *Asellus aquativus* Kaulbersz (26) describes many features of the behavior of this isopod, and especially its reaction to chemical, photic and tactile stimuli. Observations were also made on the reactions of Gammarus and Niphargus.

Kchschkowsky (27) has studied the effect of the constant electric current on various cestodes, nemerteans and annelids. Most forms reacted by a contraction of the longitudinal muscles when the anode was placed at the head end and the cathode near the tail.

Following a description of the histology of the sensory epithelium of *Microstoma caudatum*, Kepner and Taliaferro (28) have given an account of the reactions of the animal to various chemicals. The reactions were markedly influenced by variations in its " physiological tone." Removal of the ciliated pit of one side of the head caused circus movements toward the intact side. " The bilateral disposition of the ciliated pits serves to direct the animal in its movements." The same authors (29) have investigated the food taking of *Amoeba proteus*. They find much variability in the reactions to food, depending upon the condition of the animal and various external influences

Lillie and Just (30) have made several interesting observations on the breeding habits of Nereis at Woods Hole, Mass. Breeding occurs at certain periods which are influenced mainly by lunar cycles, but which are also affected by several other factors, such as time of day, weather, light and possibly temperature. During the breeding time swarms of both sexes are found swimming near the surface and when the females discharge their eggs the males discharge their sperm. The exciting factor which stimulates the males to the discharge of their sperm was shown to be some substance discharged by the egg-bearing females.

Spent females had little influence on the sperm discharge of the males, but water which had contained an egg-bearing female would quickly provoke discharge of the sperm. The substance inducing the discharge of the sperm is quite labile as it is destroyed by heat or by standing a few days in sea water.

Lillie (31) has made a study of the behavior of the spermatozoa of Nereis and Arbacia. The sperm cells of Nereis are positively chemotactic to weak solutions of CO_2 and various other acids, but they show no response to alkalis. "In contact with any solid object Nereis spermatozoa tend to carry out circus movements in an anti-clockwise direction, when fresh, but soon come to rest." They are especially attracted by substances given off by the eggs. The same is true for the sperm of Arbacia, whose general behavior resembles that of the sperm of Nereis. Chemotaxis to egg substances is probably an important factor in bringing about the fertilization of the egg.

MacCurdy (32) has shown that *Asterias forbesi* is negatively phototactic. He finds that light produces chemical changes in the starfish which were studied by examining the sea water containing specimens exposed to the light.

Metalnikow (33) finds that Paramoecia which at first ingested injurious substances came after a few hours to reject them. In another communication (34) experiments are reported on feeding infusoria with sepia and carmine. At first both sepia and carmine were ingested; after a few days the carmine was ingested in very small quantities, but the sepia was engulfed in considerable quantity.

Moore (35) finds that *Diaptomus bakeri* ordinarily indifferent to daylight becomes negative upon the addition of small amounts of caffein, strychnin, and atropin, while acids, alcohol and ether evoke a positive response.

Morse (36), who has made a detailed study of the habits of Solenomya, finds that this primitive bivalve burrows with the posterior end downward, thereby forming an exception to all other known lamellibranchs. Solenomya swims actively through the water by the combined action of the foot and valves of the shell.

Like several previous investigators, Mrázek (37) finds that Branchipus is positively phototactic and ordinarily swims on its back. This orientation was preserved after the removal of the eyes.

Orton (38, 39) has given a detailed account of the feeding mechanism and mode of feeding in Crepidula with observations on the feeding activities of various other mollusks.

Eubranchipus dadayi was found by Pearse (40) to be positively phototactic and in general positively geotactic in the light and negatively so in the dark. After mating the females resist seizure by the males and usually leave the surface and keep quiet near the bottom.

By means of several experiments on the starfish Plessner (41) has brought out several differences between the functions of the ocelli and the general photodermic sensitivity of the body. The latter serves only as a means of reaction to variations in the intensity of light. The ocelli do not enable the starfish to see images nor to detect movement, but by their means the starfish is able to direct its movements toward a slit of light or a dark object. Removal of the ocelli involves destruction of the power of locomotion to special regions of light or shade.

H. Prizbram and Matula (42) have studied the functions of the branches of an abnormal antenna of the spiny lobster Palinurus. The antenna was furnished with three flagella. Two of these conveyed sensory stimuli but did not respond by movement, but the third responded by movement to the application of stimuli.

K. Przibram (43) has pointed out certain analogies between the random movements of some of the Protozoa and Brownian movements.

Sexton and Mathews (45) have described the food habits, mating and general behavior of the young in *Gammarus chevreuxi*, a species inhabiting fresh and brackish waters around Plymouth, England.

Oregonia gracilis, like many other spider crabs, was found by Stevens (46) to possess the curious habit of decking itself with various foreign growths. Contrary to the results of Minkiewicz there was no tendency on the part of the crabs to select materials that correspond to the prevailing color of the environment. Blinded crabs decorate themselves but they show no reaction to light. Crabs which had been previously exposed to white, yellow, blue, green or red light show a manifest tendency to go toward the same kind of light when they are free to move toward any one of these colors.

By stroking gently various parts of the body of a snail in much the same way as these parts are stimulated during the mating activities Szymanski (47) has succeeded in evoking reactions which closely simulate those of mating. The studies of Szymanski (48) on the relation of tropisms to rapidity of movement were made partly on insect larvae and partly on leeches and earthworms. When the animals studied were in a condition of relative inactivity they progressed with less rapidity and made many trial movements in their sinuous course. When more active they become oriented more directly and progress with greater rapidity and in a straighter path. The author discusses different interpretations of the relation of trial movements to locomotor activity.

Torrey (50) has given a discussion of the rôle of trial movements in orientation, especially in the case of Euglena, which, it is contended, contrary to the views of Jennings and Mast, orients itself by direct responses to stimuli instead of by the method of trial and error.

Yung (51) has reached the unexpected conclusion that the eyes of snails despite their considerable degree of development are not light percipient organs. Other parts of the body, however, possess a photodermic sensibility.

Zimmermann (52) describes the movements and respiratory activities of the Galatheidea with especial reference to the structural adaptations involved.

REFERENCES

1. Allee, W. C. The Effect of Molting on Rheotaxis in Isopods. *Science n.s.*, **37**, 882-3.
2. Allee, W. C. Further Studies on Physiological States and Rheotaxis in Isopoda. *Jour. Exp. Zool.*, **15**, 257-295.
3. Balss, H. Ueber die Chemorezeption bei Garneelen. *Biol. Cent.*, **33**, 508-512.
4. Bancroft, F. W. Heliotropism, Differential Sensibility and Galvanotropism in Euglena. *Jour. Exp. Zool.*, **15**, 383-428.
5. Baunacke, W. Studien zur Frage nach der Statocystenfunktion. *Biol. Cent.*, **33**, 427-452.
6. Bohn, G. L'étude des phénomènes mnémiques chez les organismes inférieurs. *Jour. f. Psych. u. Neur.*, **20**, 199-209.
7. Brundin, M. Light Reactions of Terrestrial Amphipods. *Jour. Animal Behav.*, **3**, 334-352.
8. Brunelli, G. Recherche etologische. Osservazioni ed Esperienze sulla sinbiosi dei Paguridi e delle Attinie. *Zool. Jahrb. Abt. f. Zool. Phys.*, **34**, 1-26.
9. Buddenrock, W. v. Ueber die Funktion der Statocysten im Sande grabender Meerestiere. *Zool. Jahrb. Abt. f. Zool. Phys.*, **30**, 441-482
10. Car, L. Die Erklärung der Bewegung bei einigen Protozoen. *Biol. Cent.*, **33**, 707-711.

11. Clementi, A. Sur les mécanismes nerveux qui règlent la coordination des mouvements locomoteurs chez les Diplopodes. *Arch. Ital. Biol.*, **59**, 1-14.
12. Cole, L. J. Direction of Locomotion in the Starfish (*Asterias forbesi*). *Jour. Exp. Zool.*, **14**, 1-32.
13. Cole, L. J. Experiments on Co-ordination and Righting in the Starfish. *Biol. Bull.*, **24**, 362-369.
14. Cowles, R. P. The Habits of Some Tropical Crustacea. *Philippine Jour. Sci.*, **8**, Section D, 119-125.
15. Dubois, R. Note sur l'action de la lumière sur les Echinodermes (Oursin). *Commun 9me Congres Internat. Zool. Monaco*, Sér. 1, 8-9.
16. Erhard, H. Beitrag zur Kentniss des Lichtsinnes der Daphniden. *Biol. Cent.*, **33**, 494-496.
17. Fasten, N. The Behavior of a Parasitic Copepod, *Lernaeopoda edwardsii* Olsson. *Jour. Animal Behav.*, **3**, 36-60.
18. Franz, V. Die phototaktischen Erscheinungen im Tierreiche und ihre Rolle im Freileben der Tiere. *Zool. Jahrb. Abt. f. Zool. Phys.*, **33**, 258-286.
19. Franz, V. Aus dem Leben der Nachtschnecken. *Wochenschr. Aquar.-Terrar-Kde*, **10**, 689-690.
20. Frisch, K. v. und Kupelweiser, H. Ueber den Einfluss der Lichtfarbe auf die phototaktischen Reaktionen niedere Krebse. *Biol. Cent.*, **33**, 517-552.
21. Frölich, F. W. Vergleichende Untersuchungen über den Licht- und Farbensinn. *Deutsch. med. Wochenschr.*, **39**, 1453-1456.
22. Gee, W. The Behavior of Leeches with Especial Reference to its Modifiability. *Univ. of Calif. Pubs. Zool.*, **11**, 197-305.
23. Gee, W. Modifiability in the Behavior of the California Shore Anemone *Cribrina xanthogrammica* Brandt. *Jour. Animal Behav.*, **3**, 305-328.
24. Hess, C. Neue Untersuchungen zur vergleichenden Physiologie des Gesichtssinnes. *Zool. Jahrb. Abt. f. Zool. Phys.*, **33**, 387-440.
25. Hess, C. Eine neue Methode zur Untersuchung des Lichtsinnes bei Krebsen. *Arch. vergl. Ophthalmol.*, **4**, 52-67.
26. Kaulbersz, G. J. v. Biologische Beobachtungen an Asellus aquaticus. *Zool. Jahrb. Abt. f. Zool. Phys.*, **33**, 287-359.
27. Kchschkowsky, K. Quelques Observations sur la Physiologie des Animaux Inferieurs. *Compt. Rend. Soc. Biol.*, **74**, 700-701.
28. Kepner, W. A. and Taliaferro, W. H. Sensory Epithelium of Pharynx and Ciliated Pits of Microstoma caudatum. *Biol. Bull.*, **23**, 42-58, 1912.
29. Kepner, W. A. and Taliaferro, W. H. Reactions of *Amoeba proteus* to Food. *Biol. Bull.*, **24**, 411-428.
30. Lillie, F. R. and Just, E. E. Breeding Habits of the Heteronereis Form of Nereis limbata at Woods Hole, Mass. *Biol. Bull.*, **24**, 147-168.
31. Lillie, F. R. Studies in Fertilization. V. The Behavior of the Spermatozoa of Nereis and Arbacia with Special Reference to Egg Extractives. *Jour. Exp. Zool.*, **14**, 515-574.
32. MacCurdy, H. Some Effects of Sunlight in the Starfish. *Science n.s.*, **36**, 98-100.
33. Metalnikow, S. Sur la faculté des infusoires "d'apprendre" a choisir la nourriture. *Compt. Rend. Soc. Biol.*, **74**, 701-703.
34. Metalnikow, S. Comment les infusoires se comportent vis-a-vis des mélanges de diverses materies colorantes. *l.c.*, **74**, 704-705.
35. Moore, A. R. Negative Phototropism of Diaptomus through the Agency of Caffein, Strychnin and Atropin. *Science n.s.*, **38**, 131-133.
36 Morse, E. S. Observations on Living Solenomya. *Biol. Bull.*, **25**, 261-281.
37. Mrazek, A. Die Schwimmbewegungen von Branchipus und ihre Orientierung. *Biol. Cent.*, **33**, 700-703.
38. Orton, J. H. An account of the Natural History of the Slipper-Limpet. *Jour. Marine Biol. Assn.*, **9**, 437-443.
39. Orton, J. H. The Mode of Feeding of Crepidula, with an Account of the current-producing mechanism in the mantle cavity, and some remarks on the mode of feeding in Gastropods and Lamellibranchs. *L.c.*, **9**, 444-478.

40. Pearse, A. S. On the Habits of the Crustaceans found in Chaetopterus Tubes at Woods Hole, Mass. *Biol. Bull.*, **24**, 102-115.
41. Plessner, H. Untersuchungen über die Physiologie der Seesterne. *Zool. Jahrb. Abt. f. Zool. Phys.*, **33**, 361-386.
42. Przibram, H. and Matula, J. Reizversuche an einer dreifachen Antenne der Languste (Palinurus vulgaris Latr.). *Arch. ges. Phys.*, **153**, 406-412.
43. Przibram, K. Ueber die ungeordnete Bewegung niedere Tiere. *Arch. ges. Phys.*, **153**, 401-405.
44. Sekera, E. Beiträge zur Lebensweise der Süsswassernemertinen. *Sitz-Ber. bohm. Ges. Wiss. nat.-wiss. Classe*, 1913.
45. Sexton, E. W. and Mathews, A. Notes on the Life History of *Gammarus Chevreuxi*. *Jour. Marine Biol. Assn.*, **9**, 546-556.
46. Stevens, H. C. Acquired Specific Reactions to Color (Chromotropism) in *Oregonia gracilis*. *Jour. Animal Behav.*, **3**, 149-178.
47. Szymanski, J. S. Ein Versuch, die für das Liebesspiel charakteristischen Körperstellungen und Bewegungen bei der Weinbergschnecke künstlich hervorzurufen. *Arch. ges. Phys.*, **149**, 471-482.
48. Szymanski, J. S. Ein Beitrag zur Frage über tropische Fortbewegung. *Arch. ges. Phys.*, **154**, 343-363.
49. Szymanski, J. S. Methodisches zum Erforschen der Instinkte. *Biol. Cent.*, **33**, 260-264.
50. Torrey, H. B. Trials and Tropisms. *Science n.s.*, **37**, 873-876.
51. Young, E. La cétité des Gastéropodes pulmonés. *Arch. Sci. phys. nat. Genève, Ann.*, **118**, 77.
52. Zimmermann, K. Habit and Habitat in the Galatheidea. A Study in Adaptation. *Jour. Marine Biol. Assn.*, **10**, 84-97.

LITERATURE FOR 1913 ON THE BEHAVIOR OF SPIDERS AND INSECTS OTHER THAN ANTS

C. H. TURNER
Sumner High School, St. Louis, Missouri

TROPISMS

1. *Chemotropism.*—Trogardh (104) discusses the rôle of chemotropism in economic entomology, and Weiss (118a) dissertates on the odor preferences of insects.

2. *Geotropism.*—Weiss placed some hibernating individuals of the lace bug (*Corythuca ciliata* Say) in a glass cage in a warm room. As the temperature rose, some ascended vertical sticks and others, in the open, climbed one over the other, until there was a pillar several bugs high. As a rule, when the column was six bugs high it would sway and topple. These bugs behaved the same in sunshine and in shade and flashes of bright light did not alter their behavior. Individuals of three species of lady-bug beetles (*Adalia bipunctata*, *Coccinella 9-notata*, and *Megilla fuscilabris*) were deprived of food for from one to five minutes and then placed at the base of a fifteen-foot pole. Each climbed the pole: the first species an average height of eight feet; the second an average of one foot six inches in the sun and of seven feet six inches in the shade; the third an average of one foot four inches in the sunlight and of seven feet in the shade. The investigator considers this behavior an exhibition of negative geotropism.

3. *Phototropism.*—Heinrich (56) and Reiff (89) have discussed the reactions of butterflies and moths to light, and Holmes (61) has published a short note on the orientation of flies of the genus *Bombilius* to light.

Wodsedalek (124) has demonstrated that the phototropic responses of the Dermestidae vary at different life-history periods. Immediately after hatching the larva of *Trogoderma tarsale* is negatively phototactic and, if placed near a window, will move away from the light. This negative response persists throughout the larval period, after metamorphosis, and even for a short time after mating. Soon after ovipositing, the female becomes gradually indifferent and then positively phototactic. He has also disproved the common belief that, immediately after metamorphosis, the carpet beetle goes outside of the house to breed. He found that the carpet beetles popularly known as " buffalo moths " (*Anthrenus scrophulariae*) and the black carpet beetles (*Attagenus piceus*) respond to light in the same manner as *Trogoderma tarsale.*

By means of field observations (117), Weiss discovered that different species of mosquitoes are quite unlike in their behavior towards light. Some are equally positively and negatively phototropic, some are unequally positively and negatively phototropic and others are constantly one thing or the other. Up to a certain low intensity of light, *Culex pipiens*, *C. aurifer*, *C. canadensis*, *C. sylvetris*, *C. sallinarius*, *Anpheles maculipennis* and *Wyeomyia smithii* are positively phototropic; beyond that they are negatively so, and normally appear only at night. Near the close of the season, impregnated females of *C. pipiens* become strongly negatively phototropic and seek dark hibernating quarters. *A. crucians* is positively phototropic up to noon-day intensity of light. *A. punctipennis* responds both negatively and positively, but more often negatively. *C. perturbans* is negative in its reactions. At one place, Weiss asserts that *C. sollicitans* appears to be equally negatively and positively phototropic and that the reaction is evidently dependent upon nutrition. This does not harmonize with his statement that *C. sollicitans*, *C. cantator* and *C. taeniorhynchus*, all salt-marsh forms, are positively phototropic; but that *C. salinarius*, also a salt-marsh form, is negatively phototropic.

Holmes and McGraw (60) have devised an excellent method of studying the light responses of insects. A cylindrical jar, the bottom and side of which are covered with white paper, is covered with a cone of the same material, the apex of which conceals an electric light. A small peep hole permits the investigator to view the interior of the vessel. A circular dish containing the subject of the experiment is placed on the center of the floor of the jar. No matter which way the insect turns, the illumination is of the same intensity. Insects with one eye rendered opaque were placed in the jar and stimulated to action.

All insects did not respond in the same manner. Several beetles, of three different species, showed a tendency to turn toward the blackened eye. A Jerusalem cricket, which is negatively phototactic, when crossing from one side to the other, always turned toward the left. In a series of trials, two species of the *Tachina* fly and a specimen of the fly *Eristalis tenax* made circus movements towards the normal eye.

These same two investigators constructed a light-running turntable of cardboard. An insect was held so that its feet rested on this table and its head faced either the periphery or the center. A light was placed near one side of the turntable. Any movement on the part of the insect to escape from or to approach the light would cause the table to revolve in the opposite direction. Four species of butterflies (*Pieris raphae*, *Melitea chalcedon*, *Eurymus eyrtheme*, and *Caenonymphia california*) and two species of flies caused the disc to rotate away from the light. In the light of these two types of experiments, Holmes concludes: " It is not possible ,we believe, to construe phototaxis entirely in terms of differential sensibility. Responses to the shock of transition, whether in the direction of an increase or a decrease of stimulus, may play a part in the orientation of many forms, but the continuous stimulating influence of light appears to be, in several cases at least, the factor of major importance."

4. *Rheotropism.*—Based upon a study of *Asellus communis*, Allee (2) has reached the following conclusions concerning the responses of Isopods to currents of water: (1) In daily variations to currents the efficiency of the movements varies with the per cent of positive reactions. (2) Large variations in positive reactions are usually accompanied by similar variations in efficiency. (3) Low efficiency is accompanied by a low per cent of positive and a high per cent of indifferent responses. (4) High efficiency is always accompanied by a low per cent of indifferent responses, and usually by a low per cent of negative and a high per cent of positive responses. (5) In exceptional cases, high efficiency may be accompanied by either a low or high per cent of positive reactions. In another communication (1) the same author states that during moulting all currents are disregarded by these animals. This effect persists for about five hours after the complete casting of the skin.

5. *Thigmotropism.*—According to Weiss (118), commencing

about the middle of September, the mosquito *Culex pipiens* becomes positively thigmotactic and seeks dark quarters. After becoming acclimated to its surroundings, its normal negative phototropism is entirely replaced by positive thigmotropism. At the approach of spring the mosquito becomes positively phototropic up to a certain point.

VISUAL SENSATIONS

Hunter (63) thinks that form discrimination by animals is always pattern discrimination.

Seitz (91) discusses the vision of insects.

Karl v. Frisch's (42) recent contribution is one of the best studies extant on the color vision of insects. He arranged thirty graded discs of cardboard, extending from white to black, upon a rectangular piece of cardboard in such a manner that it was possible to insert other discs of the same size among them. So far as shades of grey were concerned, the discs were arranged on the rectangle in an irregular manner. Two yellow discs, each supporting a watchglass of honey, were placed among the grey discs. After the bees had been collecting food from these yellow discs for two days, they were removed and new yellow discs, each supporting an empty watchglass, were placed on a different part of the rectangle. Immediately these were visited by the bees; but no attention was paid to the grey discs. Bees that had been trained to forage from yellow, alighted on the yellow pencil with which Frisch was taking notes. In a similar manner bees were trained to forage from blue discs. Such bees, in four minutes, made 282 visits to the blue discs and only three to the grey. Empty watchglasses were now placed on the blue discs and similar glasses, containing sweetened water, on the grey. The bees attempted to feed from the empty dishes on the blue discs, but paid no attention to the full ones on the grey. In like manner an attempt was made to train bees to collect from red discs. Such bees visited equally the red, dark grey and black papers. Evidently bees have color vision, for they can distinguish yellow and blue from greys; but they are color blind to red.

On reading of these researches, Mrs. Ladd-Franklin (67) wrote to Frisch and asked him to make some tests to see if there was not a certain blue-green, as well as red, to which bees were color blind. He replied that he had made such tests and that bees were color blind to that portion of the spectrum. In other words, bees have a dichromatic vision, and their colors are blue and yellow. Thus their vision resembles that of the protanopic form of red-green color blindness. To Mrs. Franklin the results of these researches are gratifying, for they seem to support her theory of color vision and to militate against Hering's.

EMOTIONS

In experimenting with the common roach on a maze, Turner (105) noticed certain jumping activities which seemed to indicate an exhibition of will. He writes: "Although the jumping activity results in a plunge into the water, it resembles neither the dashes into the water made by a roach on being placed on the maze for the first time nor the falls into the water by roaches trying to run the maze. The roach pauses at the edge of the maze and explores outward and downward with its antennae. It acts as though it were trying to see something at a distance and then, after a pause, makes what an athlete would call a broad jump. Many roaches displayed this jumping behavior, but some were more prone to jump than others. * * * This jumping attitude is so characteristic that one can always tell when a roach is likely to jump. I say likely to jump instead of going to jump, because, after a roach has once jumped into the water, the jumping attitude does not always result in a spring. To see a roach, which has learned to avoid rushing off of the maze into the water and which will struggle hard to keep from slipping from the edge of a runway into the water, halt, reach outward and downward with its antennae, act as though it were trying to see what is beyond, pause and then jump is food for much thought. Have we not here a conflict of impulses and is not the jumping or refusing to jump the resultant of this conflict ? Is not such a resultant what the human psychologists call an act of will ? "

See Benard under Maternal instincts.

MATING INSTINCTS

Newell (78) describes the mating of the rice weevil, Smith (95) of a stone fly, Morgan (76) of mayflies, Gerhardt (47) of some crickets and locusts and Walker (111) of *Argia moesta*.

Fabre* states that the praying mantis of Europe is polyandrous and that the female eats her spouse. Phil and Nellie Rau (86) write that our American praying mantis (*Stegomantis carolina*) is both polyandrous and polygamous.

Fabre (39) describes the mating of several spiders. That of the angular epeira, a large garden spider, is peculiar. At nine o'clock on an August evening, the female was resting on the foundation line of her web. Cautiously a small male approached and receded several times. After a short period of this behavior, the two lovers were face to face. The female was calm and motionless; the male bristling with excitement. Timidly he touched her with a leg and then suddenly dropped from the support, spinning his drag-line as he fell. Returning, he teased her with legs and palpi. Gripping the thread with her tarsi, the female turned several somersaults and then presented the under side of her paunch to the dwarf and allowed him to fondle it with his palpi. Mating once accomplished, the male darted away, never to return.

NEST-BUILDING AND MATERNAL INSTINCTS

Coad (26) describes the oviposition of the mosquito *Culex abominator* and Fabre (39) relates many interesting things about the maternal instincts of spiders.

Buttrick (20) reports that the eggs of the salt-marsh mosquito *C. sollicitans* Walk. are deposited singly upon the mud of a salt marsh, where they remain dormant until covered by the tide or the rain. Then they hatch in a few hours and become adults in from six to fifteen days.

Parrott (81) describes the oviposition of three species of tree crickets: *Oecanthus niveus* DeGeer deposits its eggs singly at the sides of dormant buds, in the fleshy region, at the axils of the leaves of the apple, elm, plum, cherry, peach, walnut, wild crab, hawthorn, witchhazel, chestnut, red oak, maple, butternut, lilac and raspberry; *O. nigricornis* lays its eggs, in rows, upon the raspberry, blackberry, horseweed, goldenrod, willow, elder, maple, elm, sumac, grape, peach and probably others; *O. quadripunctatus* oviposits in weeds, principally the wild carrot, goldenrod and aster. The eggs are arranged in rows.

Phil and Nellie Rau (86) announce that it requires two hours

---

* Social Life in the Insect World. The Century Co., 1912, pp. 79-85.

for the mantis to construct its egg-case. When ready to oviposit, the mantis arranges herself, head downward, upon a twig. The last two abdominal segments expand and contract, otherwise the body is quiet. A ribbon of whitish substance, resembling tooth-paste, issues from the tip of the abdomen and is pressed against the twig. This ribbon soon becomes frothy. By means of the ovipositor this mass is moulded into the egg-case. (Full details are given in the paper.) While the case is being fashioned, an egg is laid in each cell. Immediately after laying, the mantis walks off a short distance, flexes her body and consumes what is left of the nest-forming material.

Hartman (55) states that the potter bee (*Eumenes belfragei* Cress.) moistens the clod with fluid from her mouth, before cutting out a piece with which to help construct on a culm of Bermuda grass her waterbottle-shaped nest. All of the work of plastering, modeling and smoothing is performed by the mandibles and the first pair of legs.

Strung along a road for about an eighth of a mile, Nichols (79) discovered numerous nests of the mining bee *Empor fusco-jubatus* Ckll. and watched the bees at work. The nest is begun as a semicircular depression. The soil is moistened with water brought in the mouth from a pond 75 yards away, is loosened by the mandibles and is cast aside by the second and third pairs of legs. As the burrow increases in depth, a portion of the removed soil is used to form a rim of moistened earth around its mouth. When the nest has been stored with pollen and the egg laid, this rim is removed and used to partly fill the burrow. This partial filling of the nest leaves a shallow depression to mark the spot. Less than 24 hours are required to complete the nest.

Bénard (8) observed a large burrowing beetle (*S. sacer* L.) rolling a ball the size of a small apple. He constructed a pen out of pieces of tile and placed the beetle and her burden therein. Immediately she seemed to lose interest in her ball. The beetle was then placed on the outside of the enclosure; but her ball of manure was left on the inside. The beetle darted off as though it were trying to escape. After making several unsteady strides, she halted and, for a moment, remained inactive. Then she returned to the tile fence that enclosed her treasure. After making several ineffective attempts to climb the wall, she tunneled beneath the tile and thus reentered into the presence of her ball. There she rested, calmly waving and cleaning her antennae. He repeated the experiment with two individuals of another species of burrowing beetles (*S. atteles*); but each scampered off as soon as she was placed on the outside of the enclosure. This is an interesting display of maternal instinct. Bénard thinks that the beetle reflected. Undoubtedly we have hesitation followed by action; but, may we not interpret it in the following manner? A stimulus from her ball, plus certain internal factors, was impelling the beetle to draw near to the ball; the grasp of the hand produced a stimulus, which, coupled with certain internal conditions, tended to induce the insect to flee. As the beetle moved farther and farther from the enclosure the effect produced by the grasp of the hand became gradually weaker and weaker until it was too feeble to affect conduct. The effect of the stimulus from the ball still persisting forced the creature to return to the enclosure. Burrowing is one of the normal instinctive activities of the burrowing beetle, hence, when unable to scale the wall, it naturally would resort to digging.

Four years ago, Roubaud,* in a single genus (*Synagris*) of potter wasps, discovered one species which stocked its burrows with enough caterpillars to last its larvae until they were ready to form pupae; another which placed a few caterpillars in each burrow and then brought more as the young needed them, and yet a third species which stored no food in its nest, but collected it and fed it to its hungry babes. Recently Wheeler (120) has discovered a mining wasp (*Aphilanthus frigidus*) which, in its maternal behavior, is intermediate between a form like *Bembex*, which captures as needed the food with which to feed her hungry larvae and those forms which stock their burrows with provisions, lay their eggs, and then pay no further attention to them. He found these wasps at Blue Hills, near Boston. Each colony covered several square yards and contained from 30 to 60 nests. The burrow, which is about one-fourth of an inch in diameter, descends obliquely and abruptly for from six to eight inches and terminates in a pocket. Similar pockets are attached to the side of the common hallway. When the ants of the genus *Formica* are having their nuptial flight, these wasps capture large numbers of the winged females. After paralyzing them and removing the wings, the wasp stores those plump ants in some of the pockets of her burrow. Later she lays an egg in one of the empty compartments. When her child has emerged, the mother brings ants from the store rooms, cuts them in two, and feeds them to the greedy larva. When this charge has developed into a pupa, she lays another egg and raises another larva in the same manner.

---

* *Ann. R. Smith. Inst.* for 1910, pp. 507-526.

FOOD PROCURING AND DEFENSIVE INSTINCTS

Newell (78) has described the feeding habits of the rice weevil, Ely (37) of *Cleonus calandroides*, Webster (114) of *Gypona octolineata* and Gillette (48) of some *Pemphiginae.*

Bishopp and King (12) assert that, with rare exceptions, the adult is the only form of the Rocky Mountain spotted fever tick that attacks man.

Linstow (68) mentions the animal diet of some caterpillars.

According to Lucy Wright Smith (95), the stone fly (*Perla immarginata*) is both carnivorous and cannibalistic; the presence of diatoms in its stomach is the only evidence of an herbivorous diet.

After stating that 1380 larvae of the Mediterranean fruit fly were obtained from 25 tropical almonds, H. H. P. Severin (92) gives a list of 38 fruits that serve as food-hosts of the larvae of this species of fruit fly.

Phil and Nellie Rau (86) give a list of the insects consumed by the mantis studied by them. These mantids are strictly carnivorous, even cannibalistic; but they will not eat robber-flies, nor stink-bugs; nor would they touch the potato beetle, except when very hungry.

These same investigators (87) have demonstrated that larval wasps often have the capacity for more food than is stored in their cells by the mother wasp. They induced one larva of *Trypoxylon albitarse* to consume two and a half and another to eat two and a fourth more spiders than had been stored in their cells.

In addition to other material, Anna Morgan (76) gives, in tabulated form, the foods of the nymphs of several species of mayflies.

According to Doane (34) the rhinoceros beetle attacks the succulent crown of the cocoanut tree. With its horn, the beetle cuts a gash in the tree and gets access to the juice, which is its only food. The succulent crown is the vital part of the tree and one or two beetles will kill a tree in a year.

A fly robbing a spider is about the last thing one would imagine, yet Frost (46) noticed three flies of the species *Desmometopa latipes* Meigen dart under the legs of a spider (*Phidippus multiformis* Emerton) and suck the juices of a bug upon which the arachnid was feeding.

It has long been known that certain tropical spiders prey upon small birds. Now Chubb (24) informs us that there is a large spider (*Thalassius spenceri* Chubb) which catches small fish and tadpoles. When this spider goes afishing, it rests its hind pair of legs upon a stone and the tips of the other six outstretched legs upon the water. With its head at about the center of the cordon of legs, the spider awaits developments. The moment a small fish or tadpole appears within range, the legs close about it, like the claws of a trap, and the mandibles deliver a deadly blow. The captive is then dragged to the top of the rock and eaten. Rev. N. Abraham saw this spider catching fish at Greytown and Rev. Pascalis Bonebery observed it catching tadpoles at Marianhill.

Wheeler (121) describes the mode of defense of the stingless bee *Trigona flaveola mediorufa* Ckll. When disturbed these bees attack *en masse*, squirting upon the offender a scalding liquid which has the odor of rancid butter. This fluid is so corrosive that the spots where it touches the skin remain sensitive for several days. Other observers to the contrary, Wheeler insists that this fluid is secreted by an anal gland or glands.

Fabre (39) describes the food-procuring habits and devices of several species of spiders. His opinion as to how young spiders secure their food is certainly peculiar. It is well known that the eggs of many spiders hatch in the fall and that the young remain in the cocoon until spring. Others emerge from the cocoon and climb upon the back of their mother and remain there for several weeks. According to Fabre's opinion these spiderlings neither increase in weight nor diminish in numbers until after they have taken their " balloon flight " in the spring. Whence comes their food ? If they do not increase in size there is no urgent need for tissue-building food; but, since they are more or less active, there is need of energy-producing material. Fabre contends that they absorb this energy directly from the sun. He bases this conclusion largely upon the fact that certain spiders take special pains to expose the cocoon, and even the uncovered young, to the rays of the sun. Although this statement appeared, in the French, several years ago, it has not been generally accepted by students of spiders. There is a leaning towards the view that the young spiders are cannibalistic. Comstock* writes: "According to the observations of Dr. B. G. Wilder some of the young of *Miranda aurantia* feed upon their weaker brothers and sisters, so that from the egg-sac that in early winter contains a large number of spiderlings there emerge in the spring a much smaller number of partly grown spiders. How general this habit of cannibalism is has not been determined. McCook states that the young of the orb-weavers prey upon each other after they leave the egg sac." If Fabre is right, this is certainly a unique form of behavior.

HIBERNATION

Biddle (9) discusses the hibernation of a butterfly (*Pyrameis atalanta*), and Pictet (83) of a moth (*Lasiocampa quercus*).

According to Ewing (38) in Oregon the lady-bug beetles (*Coccinellidae*) hibernate in pockets under stones, beneath leaves and under trash. There is a partial segregation of species.

Heretofore it has been believed that the Rocky Mountain spotted fever tick hibernates only in the nymphal and adult stages. Bishopp and King (12) inform us that this is an erroneous idea. Some hibernate in the adult stage, a few in the engorged nymphal instar, but the majority hibernate in the larval stage.

Skinner (93) observes that in winter no flies occur in the rooms of the Academy of Science of Philadelphia. With the first appearance of spring both males and females appear on the windows. All of these are fresh specimens; the ptilium not being completely retracted indicates that they have recently emerged. He concludes that flies pass the winter in the pupal stage and in no other manner.

See Weiss (117, 118) under phototropism and thigmotropism.

---

* The Spider Book. Doubleday, Page and Co., 1912, pp. 182-183.

MIGRATION

Harte (54) describes the flight of the cotton moth in 1911, and Unsicker (108) the migration of the buck moth (*Hemiluca maia*).

According to Cockerell (27), at Boulder, Colorado, July 1st, a bug (*Lygaeus facetus* Say) appeared in incalculable numbers. In some parts of the town they were so thick that they were swept up with brooms. He thinks the migration was due to the drying up of their food plants.

Ewing (38) relates that in Oregon the lady-bug beetle (*Hippodamia convergens* Guerin) spends the spring and the summer in the lower altitudes and the fall and the winter in the higher. Although there is no fixed migration, when the aphids are few large numbers of these beetles move in certain directions in search of pollen. By the middle of August all have quit the hot, dry, valleys and moved upwards.

LOCOMOTION

Claude (25) discusses jumping spiders, Hodge (59) how far flies may travel over water, and Girault (50) the swimming of certain Tettigids.

Girault (49) amputated the antennae of several different species of moths by snipping them about an eight of an inch from the head. The flight of such individuals was irregular and tended to become circular.

Fabre (39) performed some experiments demonstrating the details of the manner in which young spiders take their "balloon flights."

See Zetek (126) under technique.

ECOLOGY

Bailey (4) discusses the faunal zones of Mexico and Walker (112) those of Canada.

Vestal (110) has made an intensive ecological study of the species of grasshoppers of a limited area.

Brues (18) has been studying the distribution of the stable fly, which is the carrier of anthrax, infantile paralysis, etc. Next to the house fly, this is the most widely distributed of all insects. It occurs in every zoological region and practically throughout most of them. It is more abundant in temperate than in tropical regions.

DISEASE SPREADING ACTIVITIES

Today the search for insect spreaders of disease has proven such a fruitful field that many are attracted thereto and each year sees a number of papers published on the subject. This year such papers have been published by E. E. Austen (3), Bishopp and King (12), Bloclock and Warrington (13), Brues (18), Hadwen (53), Jennings and King (64a), Knab (66), Mitzmain (73, 74, 74a, 75), Niewenglowski (80), Sawyer and Herms (90), Townsend (100-103) and Winslow (123). Most of these papers treat of flies and mosquitoes. To the physician these papers are of great value; to the student of behavior they are slightly interesting; to the casual reader uninteresting, for they have long learned to look upon flies and mosquitoes with dread and they are not concerned about the special work of each species. However, a paper by Wheeler (121) should interest all, for he points to an unexpected source of danger. He describes a few of the habits of certain stingless bees of Central America. Buckets containing oil for destroying mosquitoes were common. One species of bee (*Trigona pallida* Lat) was seen collecting oil from the rims of these buckets and using it in making the cerumen out of which it constructed its honey-pots. Another species (*T. ruficrus corvina* Ckll.) was noticed collecting the malodorous liquid from the insides of the garbage barrels of the crematory. A third species (*T. bipunctata wheeleri* Ckll.) used human excrement in manufacturing its cerumen. Evidently, in eating the honey collected by these wild bees, one runs a great risk of contracting typhoid fever and other diseases.

MISCELLANEOUS INSTINCTS

In addition to articles mentioned elsewhere, papers on the behavior of the arachnids have been published by Popovivi (84) and Weimar (115); on the habits of the diptera by Burrell (19), Fiske (41), Guyenot (52) and Mitzmain (73); on the habits of Collembola by Collinge (29); on the behavior of the Hemiptera by Herrick (58) and Williams (122); on the habits of the Hymenoptera by Brauns (14) and Cros (31); on the habits of the Lepidoptera by Bird (10), Champion (22), Chapman (23), Frohawk (44), Strand (98) and Stauder (96); on the habits of the Orthoptera by Meijere (72).

Comstock (30) discusses the formation and uses of the silk of spiders.

Stauder (97) asserts that the caterpillars of the cabbage butterfly (*Pieris raphae*) survives the winter in the southern part of its territory.

Bénard (6) noticed a line of beetles (*Akis bacarozzo* Schrk.) approach the dead embers of a former fire. Each selected an ember of its own shape and color and, after folding its legs and antennae against its body, clung closely to the bit of wood.

Roentgen rays.—Morgan and Runner (77) aver that neither the " hard " nor the " soft " Roentgen rays have any effect upon the cigarette beetle in any stage of its existence.

Acrobatic stunts.—This year three investigators, Bénard, Turner and Wells, have described acrobatic stunts by insects. Bénard (7) noticed a number of male beetles (*Pachypus canidae* Rt.) suspended by their hind legs from blades of grass. In Hocking Co., Ohio, Wells (119) noticed flies of two different genera (*Microcerata* and *Bremia*) hanging, suspended by their hind legs, from a spider's web. Occasionally a fly would leave the web, fly about and then return and resume the suspended attitude. Turner (105) describes broad jumping by the common roach.

Speech.—Green (51) describes the humming of some midges (*Chironimidae*) and Regan (88) discusses the stridulation of a cricket (*Gryllus campestris*).

Homing.—In studying the habits of mining bees, Nichols (79) found that some bees flew directly to the nest and that others had much trouble in finding it; some were disturbed by the presence of the investigator and others were not.

By altering the environment in the immediate vicinity of the nest of certain wasps (*Sceliphron caementarius*), Phil and Nellie Rau (87) were able to " confuse " the home-coming wasps.

Letisimulation.—Weiss (118b) describes the death feigning of the rice weevil (*Calandra oryzae*); Girault (49) finds that the skin beetle (*Trox*) letisimulates as soon as touched and that it remains rigid and still; and Newell (78) states that the rice weevil (*Lissorhoptus simplex* Say) frequently letisimulates.

MEMORY AND ASSOCIATION

Hartman (55) noticed that a certain potter wasp required twenty loads of mud to construct its nest. Each time it returned to the same clod for its load.

Turner (105) tested the ability of the common roach to learn a maze similar to those used so much by students of vertebrate behavior. The maze used was open, *i.e.*, there were no walls surrounding the runways. The maze contained several blind alleys, some of which were complex. When in use, the maze was supported by means of slender glass pillars above a wide pan of water, so that if the roach fell off of the runways it was sure to fall into water. The roach to be tested was always placed on the same portion of the maze, and before each trial the runways were washed with alcohol, to remove any odor that may have been left there by a roach. When a roach was placed on the maze for the first time, it always made many mistakes, such as rushing into or falling into the water, going into blind alleys and retracing its steps when on the right pathway. Gradually these errors were eliminated and the roach took the shortest path from the place where she was placed on the maze to its cage, which was reached by a paper inclined plane. The investigator draws the following conclusions: (1) By arranging the trials at intervals of half an hour, a roach may be taught, within a day, to run the maze. (2) The gradual manner in which errors are eliminated would cause one to conclude that the roach learns to run the maze by the trial and error method; yet, in so doing, it utilizes sense stimuli. This is evidenced by the careful manner in which it examines (often over and over again) the corners and the edges of the maze and the space adjacent thereto. (3) At times the roach acts as though experiencing the emotion the psychologists call will. (4) Although the effects of training persist for a long time, yet the memory of the roach is poor; for, after an interval of twelve hours, marked lapses are noticed. (5) In its toilet activities the behavior of the roach resembles very much the toilet-making activities of the cat. (6) In their behavior on the maze roaches display marked individuality.

TECHNIQUE

Hentschell (57) discusses insect aquaria, and Zetek (126) describes, in detail, how to raise mosquitoes in aquaria.

Hunter (62) describes and illustrates an apparatus which will maintain constant or variable temperatures from 60° F. to -10° F.

In his experiments on the flight of mosquitoes, Zetek (126) devised a method which may prove of value to students of other groups of insects. The mosquitoes were sprayed with anilin dye and then set free. Later insects were captured, both by hand and by the aid of traps. These were placed on a piece of glass that rested on a white blotter. Each mosquito was moistened with a solution composed of three parts of glycerine, three parts of alcohol and one part of chloroform. If the sprayed individual was one of the marked specimens the dye would diffuse out.

See Holmes and McGraw (60) under phototropism.

REFERENCES

1. Allee, W. C. The Effects of Moulting on Rheotaxis in Isopods. *Science*, **37**, 882-883.
2. Allee, W. C. Further Studies on the Physiological States and Rheotaxis in Isopoda. *Jour. of Exper. Zool.*, **15**, 257-295.
3. Austen, Ernst E. The House Fly as a Danger to Health. Its Life History and How to Deal with It. *British Museum (Natural Hist.) Economic Series*, No. 1, 1-12.
4. Bailey, V. Life Zones and Crop Zones of New Mexico. *U. S. Dept. of Agriculture, Biol. Survey N. Amer.*, No. 35.
5. Barber, H. S. The Remarkable Life-history of a New Family (*Micromalthidiae*) of Beetles. *Jour. N. Y. Entom. Soc.*, **26**, 185-190.
6. Benard, G. L'Akis Bacarozzo Schrk. (*Coleoptera Tenebrionidae*). Observation sur ses Moeurs. *Bull. du Museum National D'Histoire Naturelle*, 276-277.
7. Benard, G. Le Pachydus Canidae Rt. (*Coléopt. Scarabaeidae*) Attitudes Singulieres des Males. *Bull. du Museum National D'Histoire Naturelle*, 275-276.
8. Benard, G. Observation Nouvelle sur le *Scarabaeus sacre* L. Un Acte Réfléchi. *Bull. du Museum National D'Histoire Naturelle*, 233-235.
9. Biddle, E. Hibernation of *Pyrameis atalanta*. *The Entomologist*, London, 171.
10. Bird, H. On the Larval Habits of Two Species of Oligia. *Insecutor Inscitiae Menseruus.* A monthly journal of entomology, Washington, D. C. 1, 123-124.
11. Bishopp and Wood. The Biology of some North American Ticks of the Genus *Dermacentor*. *Parisitology*, Cambridge, Eng., **6**, 153-187.
12. Bishopp, F. C. and King, W. V. Additional Notes on the Biology of the Rocky Mountain Spotted Fever Tick. *Jour. of Econ. Entom.*, **6**, 200-211.
13. Bloclock, B. and Warrington, Yorke. The Trypanosomes Causing Durine (Mal de coit or Beschälseuche). *Proc. Royal Soc.*, Series B, **87**, 89-95.
14. Brauns, H. Biologie Südafricanischer Apiden. *Zeit. f. Wiss. Insektenbiologie*, **9**, 116-120.
15. Brierley, W. B. The Structure and Life History of *Leptosphaeria Lemineae* (Cohn). *Mem. and Proc. of the Manchester Literary and Phil. Soc.*, 1912-13, Mem. VIII, 1-24.
16. Brocher, F. Recherches sur la Respiration des Insectes Aquatiques. *Ann. Biologie Lacustre*, Brussels, **5**, 218-258.
17. Browne, F. B. The Life History of a Water Beetle. *Nature*, London, **92**, 20-24.
18. Brues, C. T. The Geographical Distribution of the Stable Fly (*Stomoxys calcitrans*). *Jour. of Econ. Entom.*, **6**, 459-477.

19. Burrell, A. C. Economic and Biologic Notes on the Giant Midge (*Chironomus plumosus*). *Bull. Wis. Nat. Hist. Soc.*, **10**, 124-163.

20. Buttrick, P. L. The Effect of Tides and Rainfall on the Breeding of Salt Marsh Mosquitoes. *Jour. of Econ. Entom.*, **6**, 352-359.

21. Chaine, J. Les Ilots der Termites. *Compte Rendu Acad. Sc.*, Paris, **107**, 650-653.

22. Champion, G. C. Note on the Larva of Scirtes. *The Entom. Mo. Mag.*, London, 32-33.

23. Chapman, T. A. Pupal Moult of *Agriades coridon.* The Maxillary Pocket of Plebeiid Pupae. *The Entom. Record*, London, 163-167.

24. Chubb, E. C. Fish Eating Habits of a Spider. *Nature*, **91**, 136.

25. Claude, D. L'Araignee Santeuse. *La Nature*, Paris, **41**, 305-306.

26. Coad, B. R. Oviposition Habits of *Culex abdominator.* *The Canad. Entom.*, **45**, 265-266.

27. Cockerell, T. D. A. Swarming of Hemiptera. *Jour. of Econ. Entom.*, **6**, 426.

28. Cockle, J. W. Strange Action of *Bombus occidentalis.* *Psyche*, **20**, 347-348.

29. Collinge, W. E. Collembola Damaging Pine Trees. *Jour. of Econ. Biol.*, London, **8**, 99.

30. Comstock, J. H. The Silk of Spiders and Its Uses. *Second Intern. Entom. Congr.*, **2**, 1-10.

31. Cros, A. Le Sitaris fipes Ses Moeurs, son Evolution. *La Feuille des Jeunes Naturalistes*, Paris, **43**, 173-177.

32. Davis, J. J. The Life Cycle of *Lachnosterna tristis.* *Jour. of Econ. Entom.*, 6, 276-278.

33. Doane, R. W. An Annotated List of the Literature on Insects and Disease for the Year 1912. *Jour. of Econ. Entom.*, **6**, 366-385.

34. Doane, R. W. The Rhinoceros Beetle (*Oryctes rhinoceros* L.) in Samoa. *Jour. of Econ. Entom.*, **6**, 437-442.

35. Dutt, G. R. Life Histories of Indian Hymenoptera. *Memoirs, Dept. of Agri. of India*, **4**, 183-267.

36. Eckardt, W. R. Die Wetterpropheten aus dem Reiche der Lufte. *Entom Zeitschrift*, **27**, 106-107.

37. Ely, C. R. The Food Plant of *Cleonus calandroides.* *Proc. Entom. Soc. of Washington*, **15**, 104-105.

38. Ewing, H. E. Notes on Oregon Coccinellidae. *Jour. of Econ. Entom.*, **6**, 404-407.

39. Fabre, J. H. The Life of the Spider. Translated by Alexander Teixeira de Mattos. New York, Dodd, Mead and Co., 404 pp.

40. Fabre, J. H. The Life of the Fly. Translated by Alexander Teixeira de Mattos. New York, Dodd, Mead and Co., 477 pp.

41. Fiske, W. F. The Binomics of *Glossina;* A Review with Hypothetical Conclusions. *Bull. Entom. Research*, London, **4**, 95-111.

42. Frisch, Karl von. Zur Frage nach dem Fabensinn der Tiere. *Gesellschaft d. Naturforscher u. Arzte*, Verhandlun, 1913, 1-6.

43. Frisch, Karl von. Ueber den Farbensinn der Beinen und die Blumenfarben. *Munchener Medizinischen Wochenschrift*, 1-10.

44. Frohawk, F. W. Life History of *Argynnis hecate.* *The Entomologist*, London, 249-252.

45. Frohawk, F. W. The Life History of *Coenonympha tiphon.* *The Entomologist*, London, 145-148.

46. Frost, C. A. Peculiar Habits of Small Diptera. *Psyche*, **20**, 37.

47. Gerhardt, U. Copulation und Spermatophoren von Grilliden und Locustiden. *Zool. Jahrb.*, **35**, 415-532.

48. Gillette, C. P. Some Pemphiginae Attacking Species of Populus in Colorado. *Ann. Entom. Soc. Amer.*, **6**, 485-493.

49. Girault, A. A. Fragments of North American Insects, VI. *Entom News*, **24**, 338-344.

50. Girault, A. A. Notes on the Habits of a Few Insects: 1. Flies Reacting to the Odor of Carbide. 2. Tettigids Swimming. 3. Jealousy in Pentatomids. *Queensland Naturalist*, Brisbane, **1**, 254-255.

51. Green, E. E. On the Humming of Chironomidae. *The Entom. Mon. Mag.*, London, 37.
52. Guyenot, E. Etudes Biologiques sur une Mouche *Drosophila ampelophila. Jour. of Ex. Zool.*, **15,** 267-274.
53. Hadwen, S. On "Tick Paralysis" in Sheep and Man Following the Bite of *Dermacentor venustus. Parasitology*, **6,** 283-297.
54. Harte, C. R. Observations Regarding Flight of the Cotton Moth in 1911. *Jour. Econ. Entom.*, **6,** 389-395.
55. Hartman, Carl. The Habits of *Eumenes belfragei*, Cress. *Jour. Animal Behav.*, **3,** 353-360.
56. Heinrich, R. Der Schmetterlingsfang am Licht. *Intern. Entom. Zs.*, **6,** 235-237, 252-254.
57. Hentschell, H. Das Insekten Aquarium. *Intern. Entom. Zs.*, **7,** 141-142.
58. Herrick, G. W. Some Scale Insects of Mississippi, with Notes on Certain Species from Texas. *Miss. Agri. Ex. Station, Agricultural College, Tech. Bull.*, No. 2.
59. Hodge, C. F. The Distance House Flies, Blue Bottle and Stable Flies May Travel Over Water. *Science*, **66,** 512-513.
60. Holmes, S. J. and McGraw, K. W. Some Experiments on the Method of Orientation to Light. *Jour. Animal Behav.*, **3,** 367-373.
61. Holmes, S. J. Note on the Orientation of *Bombilius* to Light. *Science*, **38,** 230.
62. Hunter, W. S. Apparatus for Maintenance of Thermal Climatic Conditions. *Jour. Econ. Entom.*, **6,** 196-197.
63. Hunter, W. S. The Question of Form Perception. *Jour. Animal Behav.*, **3,** 329-333.
64. Imms, A. D. Contributions to a Knowledge of the Structure and Biology of Some Indian Insects. *Trans. Linn. Soc.*, London, **11,** 167-195.
64a. Jennings and King. An Intensive Study of Insects as a Possible Etiologic Factor in Pellagra. *Amer. Jour. Med. Sci.*, **146,** 411-441.
65. Klein, F. Biologische Beobachtungen and *Chrysomela fastuosa. Entom. Blatt.*. 122-128.
66. Knab, F. The Contensions Regarding " Forest Malaria." *Proc. Entom. Soc. Wash.*, **15,** 110-118.
67. Ladd-Franklin, C. A Nonchromatic Region in the Spectrum for Bees. *Science*, **38,** 850-852.
68. Linstow, Dr. Animalische Nahrung für Raupen. *Intern. Entom. Zeit.*, **7,** 27-28.
69. Lovell, J. H. A Vernal Bee (*Colletes inaequalis*). *Psyche*, **20,** 147-148.
70. Lutz, A. The Insect Host of Forest Malaria. *Proc. Entom. Soc of Wash.*, **15,** 108-109.
71. Mansion, J. Les Larves des Dipteres Vivent Elles dans le Formol? *La Feuille des Jeunes Naturalistes*, Paris, **43,** 168-172.
72. Meijere, J. C. H. de. Ueber das Ausschluppen der Mantiden. *Tidschrift voor Entom.*, **16,** 62-68.
73. Mitzmain, M. B. The Biology of *Tabanus Striatus*, the Horsefly of the Philippines. *Philippine Jour. of Sci.*, **8,** Sec. B, 197-222.
74. Mitzmain, M. B. The Role of *Stomoxys calcitrans* in the Transmission of *Trypanosoma Evansi. Philippine Jour. of Sci.*, **7,** Sec. B, 475-520.
74a. Mitzmain, M. B. The Bionomics of *Stomoxys calcitrans*; a Preliminary Account. *Philippine Jour. of Sci.*, **8,** Sec. B, 29-48.
75. Mitzmain, M. B. The Surra-conveying Fly of the Philippines and some Factors Concerned in Control Measures. *Philippine Agri. Rev.*, **6,** 371-379.
76. Morgan, Anna H. A Contribution to the Biology of May-flies. *Ann. Entom. Soc. of Amer.*, **6,** 271-413.
77. Morgan, A. C. and Runner, G. A. Some Experiments with the Roentgen Rays upon the Cigarette Beetle, *Lasioderma serricorne* Fabr. *Jour. Econ. Entom.*, **6,** 226-230.
78. Newell, Wilmon. Notes on the Rice Weevil (*Lissorhoptrus simplex* Say) and Its Control. *Jour. Econ. Entom.*, **6,** 55-61.

79. Nichols, M. L. Some Observations on the Nesting Habits of the Mining Bee, *Empor fuscojubatus* Ckll. *Psyche*, **20**, 107-112.
80. Niewenglowski, G. H. La Transmission des Maladies par les Mouches. *La Naturaliste Canadien*, **40**, 33-38.
81. Parrott, R. J. and Fulton, B. B. Notes on Tree Crickets. *Jour. Econ. Entom.*, **6**, 177-180.
82. Quelques Detailes sur les Moeurs et la Coloration du *Pytho depressus*. *Bull. Soc. Entom. de France*, Paris, 205-207.
83. Pictet, A. Recherches Experimentales sur L'Hibernation de *Lasiocampa quercus*. Recherches Experimentales sur la resistance au Froid et la Longevity des L. a L'Etat Adulte. *Bull. Soc. Lepidopterologique de Geneve*, **2**, 179-212.
84. Popovivi-Baznosanu, A. *Trichotarsus osmiae*. *Archiv. Zool. Exp. et Gen.*, Paris, **52**, 32-42.
85. Prochnow, Oskar. Färbunsanpassungen. Kritischer Sammelbericht über Arbeiten aus dem Gebiete der Schutz-, Warn-, Schreck-, und Pseudo-Warm-farbung aus der Jahren 1905-1911. nebst einer Zusammenfassenden Einleitung. *Zeit. f. Wiss. Insektenbiologie*, **9**, 63-68, 100-102, 138-140, 165-168, 215-220, 281-284, 313-317, 350-352, 386-388.
86. Rau, Phil and Nellie. The Biology of *Stegomantis carolina*. *Trans. Acad. of Sci. St. Louis*, **22**, 1-58, pls. I-XVIII.
87. Rau, Phil and Nellie. Some Observations on Mud Wasps. *Entom. News*. **24**, 392-404.
88. Regen, J. Untersuchungen über die Stridulation von *Gryllus campestris*. *Zool. Anz.*, **42**, 143-144.
89. Reiff, W. Ueber den Schmetterlingsfang am Licht. *Intern. Entom. Zeitschrift*, **6**, 310-311.
90. Sawyer and Herms. Attempts to Transmit Poliomyelitis by Means of the Stable Fly (*Stomoxys calcitrans*). *Jour. Amer. Med. Assn.*, 461-466.
91. Seitz, A. On the Sense of Vision of Insects. *Second Intern. Entom. Congr.*, **2**, 198-204.
92. Severin, H. H. P. The Life History of the Mediterranean Fruit Fly (*Ceratitis capitata* Wied.) with a List of Fruits Attacked in the Hawaiian Islands. *Jour. Econ. Entom.*, **6**, 399-403.
93. Skinner, Henry. How Does the Housefly Pass the Winter? *Entom. News*, **24**, 303-304.
94. Sladen, F. W. L. Bee with Pollinia Attached to its Feet. *Ottawa Naturalist*, **26**, 116-117.
95. Smith, Lucy Wright. The Biology of *Perla immarginata* Say. *Ann. Entom. Soc. of Amer.*, **6**, 203-212.
96. Stauder, H. Beitrage zur Biologie der Raupen von *Lysmantria dispar* und *Phalacropteryx praecellens*. *Zeit. f. Wiss. Insektenbiologie*, **9**, 148-151.
97. Stauder, H. Ueberwinterung bei *Picris rapae* Raupe in Suden des Fluggebietes der Art. *Zeit. f. Wiss. Insektbiol.*, **9**, 209.
98. Strand, E. Zur Biologie von *Diapalpus congregarius*. *Archiv. f. Naturgesch.*, Ab. A, H. 2, 121-122.
99. Swingle, L. D. The Life History of the Sheep Tick (*Melophagus ovinus*). *Univ. of Wyo. Agric. Exp. Station*, Bull. 99.
100. Townsend, C. H. T. A Phlebotomus the Practically Certain Carrier of Verruga. *Science*, **38**, 194-195.
101. Townsend, C. H. T. Muscoid Parasites of the Cotton-Stainer and Other Lygaeids. *Psyche*, **20**, 91-94.
102. Townsend, C. H. T. Possible and Probable Etiology and Transmission of Verruga Fever. *Jour. Econ. Entom.*, **6**, 211-225.
103. Townsend, C. H. T. Progress in the Study of Verruga Transmission by Blood Suckers. *Bull. Entom. Research*, London, **4**, 125-128.
104. Trogardh, I. On the Chemotropism of Insects and Its Significance for Economic Entomology. *Bull. Entom. Research*, London, **4**, 113-117.
105. Turner, C. H. Behavior of the Common Roach (*Periplaneta orientalis* L.) on an Open Maze. *Biol. Bull.*, **25**, 348-365.

106. Turner, C. H. Literature for 1912 on the Behavior of Spiders and Insects Other than Ants. *Jour. Animal Behav.*, **3**, 401-428.
107. Turner, C. H. Recent Literature on the Behavior of the Higher Invertebrates. *Psy. Bull.*, **10**, 307-317.
108. Unsicker, Dr. *Hemiluca maja*, Ihre Lebenweise und Ihre Vanwandten. *Zeit. f. Wiss. Insektbiol.*, **9**, 208-209.
109. Urban, C. Beitrage zur Lebensgeschichte der Käfer. *Entom. Blaett.*, 16-19.
110. Vestal, A. C. Local Distribution of Grasshoppers in Relation to Plant Associations. *Biol. Bull.*, **25**, 141-180.
111. Walker, E. M. Mutual Adaptation of the Sexes in *Argia moesta*. *The Canad. Entom.*, **45**, 277-279.
112. Walker, E. M. Faunal Zones of Canada. *Ann. Rept. Entom. Soc. of Ontario*, 1912, 26-33.
113. Walton, W. R. Efficiency of the Tachinid Parasite on the Last Instar of *Laphyma.Proc. Entom. Soc. of Washington*, **15**, 128-131.
114. Notes on *Gypona octolineata* Say. *Jour. of Econ. Entom.*, **6**, 409-413.
115. Weimar, E. R. Beitrage zur Biologie des Wasserbaren *Macerobiotus lacustris. Mikrokosmos Zeit. f. d. Praktische Batatigung Aller Naturfreunde*, **7**, 153-159.
116. Weiss, H. B. Notes on the Negative Geotropism of *Corythuca ciliata* Say, *Adalia bipunctata* L., *Coccinella* 9-*notata* Hbst., and *Megilla fuscilabris* Muls. *Jour. Econ. Entom.*, **6**, 407-409.
117. Weiss, H. B. Note on the Phototropism of Certain Mosquitoes. *Entom. News*, **24**, 12-13.
118. Weiss, H. B. Positive Thigmotropism of *Culex pipiens* in Hibernation. *Psyche*, **20**, 36.
118a. Weiss, H. B. Odor Preferences in Insects. *The Canad. Entom.*, **45**, 302-304.
118b. Weiss, H. B. Notes on the Death Feint of *Calandra oryzae*. *The Canad. Entom.*, **45**, 135-137.
119. Wells, B. W. An Acrobatic Fly. *Jour. Econ. Entom.*, **6**, 330.
120. Wheeler, W. M. A Solitary Wasp (*Aphilanthops frigidus*) that Provisions Its Nest with Queen Ants. *Jour. Animal Behavior*, **3**, 374-387.
121. Wheeler, W. M. Notes on the Habits of Certain Central American Stingless Bees. *Psyche*, **20**, 1-9.
122. Williams, C. B. Some Biological Notes on *Raphidia maculicollis*. *The Entomologist*, London, 6-8.
123. Winslow, C. E. A. An Insect-borne Disease. Infant Paralysis. (Illustrated from Models of *Stomoxys* and *Musca*.) *The Amer. Mus. Jour.*, New York, 229-235.
124. Wodsedalek, J. E. The Relation of Certain Dermestidae to Light in Different Periods of Their Life History. *Jour. Animal Behav.*, **3**, 61-64.
125. Zamber, C. Moeurs et Metamorphoses des Insects: *Coleopteres*. *Ann. Soc. Linneene du Lyon*, **56**, 1-49, 59, 161.
126. Zetek, J. Determination of the Flight of Mosquitoes. *Ann. Entom. Soc. of Amer.*, **6**, 5-21.

LITERATURE FOR 1913 ON THE BEHAVIOR OF VERTEBRATES

STELLA B. VINCENT
University of Chicago

VISION

Mammals. The work on vision, for 1913, although not so extended as it has been in some previous years, is interesting. The Watsons (57) report some experiments with rodents in which they used the spectral light apparatus described in the Yerkes-Watson monograph. They wished to discover whether the differential response, in the use of color, was made on the basis of wave length. Two animals were trained to react positively to red when red and green were presented simultaneously; but, in later testing, it was found that, when the intensity was varied or only one color was presented, the animals were neglecting red and reacting to green alone. "One might increase the green light enormously or eliminate the red altogether without changing the accuracy of the responses. When, however, the intensity of the green approaches the threshhold—a disturbance immediately manifests itself." Two white rats, the one trained for yellow and the other for blue, and a black-white rat and a gray Belgian hare, trained for blue, failed to perfect a discrimination in over 500 trials when both stimuli were present at full intensity. There was a rapid rise of the habit, however, when only one, positive, stimulus was given. The second stimulus was then introduced in gradually increasing intensities. In the cases where the blue was the positive stimulus the association was maintained up to nearly equal intensities. The rat trained for yellow was disturbed by blue when its energy was only one-eighteenth that of the yellow. They conclude that the long wave lengths offer very slight, if any, visual stimulation to rodents and that the response was probably made to differences of intensity.

The difficulties of such work and the dangers of premature conclusions are illustrated in the critique of Cole's experiments with raccoons made by Gregg and McPheeters (22). These men repeated Cole's work in which the animals were taught to discriminate between two temporal series of stimuli. As will be remembered colored cards were used. They were raised above a screen by a series of levers. The animals were taught to react positively to W.B.R. and negatively to R.R.R. Cole concluded that the discrimination was made by means of vision, that it was presumably based upon brightness and that all three presentations of the series were effectual. He thought that the " carrying over " of the stimulating effects of the first two cards till the final response must be the result of an imaginal process. Only two raccoons were used in the Chicago experiments. One of these learned to respond in a fashion similar to Cole's animals. A control series of experiments included: the exchange of R.W. cards, change of operators, use of fresh color cards, washing levers, change of lever order, substitution of entirely different colors, use of bare levers without cards, and use of glass screen before levers. The conclusion was reached that the discrimination was based primarily upon an apprehension of the relative spatial position of the levers which was mediated through nose contact in active, not passive, touch. The discrimination seemed to be based exclusively upon the difference between the first members of the groups which resulted in the setting up of certain motor attitudes. The third member was common to the two groups and hence could not serve as a basis for discrimination but it did serve to release the discriminative response which had been set up by the previous stimuli. The functional relation of the second member of the series was not worked out. The authors do not deny that raccoons have and may use visual images but say that Cole's experiments do not prove their existence as the " carrying over " may be by means of motor attitudes.

In Johnson's (29) work with dogs, some of the puppies were made temporarily blind by having their eyelids sewed together before they had gained their sight. In the latter part of his monograph he attempts to give an account of the learning time and the learning methods of these blind dogs as compared with normal dogs. The problem was the opening of cage doors, having different kinds of latches, under the stimulus of hunger.

The latches were the spoon dip, turn button, lift bar, slide bar, peg-in-hole and bobbin and string. Some of the doors swung inward and some outward. His program included (1) the learning of three boxes by each dog while still blind, (2) after learning, a test for any disturbance following the darkening of the room; (3) a test of rotation of the box; (4) a retention test after 60 days; (5) the learning of three other problem boxes after the eyes had been opened. As a matter of fact there was so little difference between the results of the blind and the normal dogs that the fifth part of the program was not undertaken. The test in the darkness showed a slight disturbance in the blind animals, indicating that the light evidently had some stimulating effect. The disturbance was much greater in the normal dog. The blind and normal dogs were equally affected by the change in orientation. The retention tests for the two groups gave similar results. To the reviewer it seems unfortunate that the last part of the plan was abandoned. The mere fact that blind and normal animals give the same results in time and accuracy in a problem does not prove that the mode of procedure or the sensory control is the same. It is not asserted to be so in this case. But quite startling results often follow from the addition of a stimulus as well as from its elimination and it is to be regretted that when trained and operated animals were at hand this step was not taken.

Amphibians. The responses of young toads to intense and moderately intense artificial light, to strong and weak diffuse daylight, to sunlight and to colored light were studied by Riley (47) in a long, careful series of experiments. He sums up his work as follows: "The young toads respond negatively to the light from a projection lantern with an approximate illumination of 10,000 ca.m. within the field of the experimentation." They respond positively to incandescent light with an illumination of approximately 44 ca.m., to strong and weak diffuse daylight and to sunlight. "Except in the diffuse daylight the animals jump toward the source of the illumination in a comparatively straight line." "It is not improbable that both light intensity and ray direction in the field are factors in these photic responses. During orientation light intensity may play the more important rôle, while the rays in the field may act as a guiding factor after orientation is complete though this does not necessarily do away with the effect of intensity."

Hess had previously shown that amphibian vision is like human, *i.e.*, under dark adaptation the long wave end is shortened and the region of greatest brightness is pushed toward the shorter wave end. Himstedt and Nagel had confirmed this conclusion by a study of the action currents of the eye. Now Babák (2), by means of the breathing method described in this journal, 1913, Nov.-Dec., shows the same thing but adds additional curious facts. By this method the stimulating effect of V seemed extraordinarily great. Even in weak intensities it was stronger than the G. He says that the filter apparatus was, of course, not absolute, yet undeniably R and V equal in brightness had different stimulus values. R had a very weak, V a very strong influence on the breathing activity. W light had a slighter stimulus value than V. It seemed to be the resultant of the RG and V effects. He thinks that this result is probably caused by the ultra-violet rays while the long thermal rays have a practically negligible effect.

Fishes. The facts as to the color vision of fish are still controverted points in which C. Hess (26, 27) and von Frisch (17, 18, 19, 20, 21) are the principal opponents. A considerable number of papers have appeared which will be discussed together since nothing is gained by separate reviews and since in each new article the whole argument is repeated with additional matter. To von Frisch the chromatic adaptation of fishes to the color of the background against which they lie is an evidence of color vision. He discusses this adaptation at length and shows how it is due to the expansion and contraction of the pigment cells. This reaction, he believes, depends upon the nervous system and he finds a center in the brain anterior to the cord whose stimulation will cause such changes. The study is continued by means of nerve section, histological methods, etc. The reaction to yellow ground was only found in those fishes which could see. *Phoxinus laevis L.* reacted to yellow ground by an expansion of R and Y pigment cells but to G, Blue, or V ground in the same way as to gray. This reaction was, therefore, due to brightness. He used blind *Crenilabrus roissali*, five groups of five fish each, and had them four weeks under experimentation.

Fish were kept for long periods in aquaria with double walls, the spaces between being filled with Nagle's color solution, and the same results were obtained. The blind fish were not affected by the red or yellow background hence pigment growth is not due to the effect of colored light. This work was demonstrated before five people. Von Frisch thinks that the adaptation to brightness does not depend upon light intensity alone but also upon color contrast and is a higher reaction than that to color as is proved by its quickness and its accuracy. He believes, too, that the expansion of the red pigment cells is also, within wide limits, independent of the brightness values of the bottom and depends alone on its color value.

The *Hochzeitkleid* is adduced as a strong bit of evidence of the color vision of fish. Why, it is asked, should they take on these brilliant colors at spawning time if these colors are of no value in sexual selection.

Von Frisch as well as Hess made experiments with colored food. When his fish which had been trained for yellow food were offered a series of gray papers together with yellow upon a gray background, they always snapped at the yellow, he says, and never at the gray. They chose red papers and not black upon a gray ground. In this respect they differ from bees. They frequently snapped at purple and yellow-green. He gives the numbers of his papers and had the results demonstrated before five people. He also fed his fish from a series of colored tubes so arranged that food could be placed in the top and the tubes sunk in the water. *Phoxinus laevis* could distinguish red-yellow, green and blue from gray one and one-half centimeters below the surface. The red and the yellow were confused. He explains this by saying that the red pigment is essentially a sex color but that later it functions in the same way as yellow. The protective colors are on the back, the sex colors on the abdomen.

Hess admits, as all must, the chromatic adaptation in fishes but criticises its significance as a proof of color vision. He also disputes some of von Frisch's facts and questions certain methods which he uses. Some apparatus was constructed by Hess by means of which two bowls containing fish could be lighted from below with diffused lights of known strength. The observer could not detect the slightest difference in the appearance of the fish even when one light was five or six times the strength of the other. Yet, he says, fish are known to perceive differences in brightness which are as 1 : 1.23. Hence von Frisch's assumption that the color of a fish proves that it recognizes this color as identical with that of its background is unproven. Hess believes that color adaptation may be due to brightness or to the intensity values of light or it may not have a visual cause at all and he cites Dorflein's experiments with crabs which were kept in the dark and yet turned red. Crenilabri were also used by Hess. Part of the fish were put in a ruby glass aquarium with a background of white walls and the others in a black aquarium covered with a black cloth. After eight days it is said, no observer could see any difference in the fish. Fish were trained by him for yellow food but could not distinguish it against a blue ground or a gray of the same brightness. He thinks Washburn and Bentley could draw no conclusions from their work on the color vision of fish because of their method.

He insists that a protective device to be effective must take place in a few minutes and not in a few hours. The facts of color adaptation in the human retina are alleged as against the assumption.

In answer to the evidence of the *Hochzeitkleid* for vision he declares that fish which spawn at a depth of from six to eight meters cannot see red. Red can be seen directly at from three to four meters but viewed obliquely it is brownish or grayish. Markings, therefore, can be of little value in deep water and yet fishes which spawn at great depths have these markings. In all his work Hess clings to the belief that fish have the vision of color-blind men.

Von Frisch in reply to this last argument gives a long list of fish with the depths at which they spawn and the time of spawning, *i.e.*, night or day. He admits that many of the fish which spawn at night have brilliant colors. But, he says, when it is seen that most varieties take on color at spawning time, and at no other time, and that it is always characteristic of those which spawn in shallows, where conditions are favorable for the perception of brilliant color, it is only natural to believe that the wedding dress is an attractive cloak.

Birds. Bingham (4) investigated the perception of size and form in chickens, using the Yerkes-Watson apparatus, which is described in the Behavior Monograph (1911, vol. 1, no. 2).

With this apparatus the size, form, and relative position of the stimulating object as well as its brightness can be independently varied and controlled. The first experiments were concerned with size—the discrimination of circles of unequal size. The stimuli were at first complex, differing in form, size and brightness. Little by little they were changed until the only distinction was that of size. Under these circumstances the birds learned to discriminate between circles whose diameter differed from the standard six centimeters by one-fourth to one-sixth. The control tests left no doubt in the minds of the experimenter that this discrimination was made entirely on the basis of size. He also succeeded in teaching one bird to distinguish between a circle and a triangle of equal area. The bird was unable, however, to make this discrimination when the relative positions of the forms were changed and he thinks the power depended upon the unequal stimulation of different parts of the retina.

Hunter (28) in discussing this bit of experimentation, together with some other work, emphasizes the necessity of considering the background in all such investigations. The position is taken that the vision of animals is probably what may be called a pattern vision, that animals see a form within an outlined visual field which must also be varied for perfect control. Real form discrimination he thinks is a more abstract and later mode of perception.

The dual visual theory assumes that the cones of the retina function for daylight and the rods for twilight vision and that only the cones have the power of adaptation. A study of the eyes of nocturnal animals would seem valuable here. Such studies have been made before. Hess investigated the pupil-motor valence of the dark adapted eye, but did not make any comparisons under conditions of bright adaptation. Katz and Révész (30) do this in a study of the eyes of owls. They used the light from a Nernst lamp filtered through colored gelatine plates. There was a variable opening for the light which could be easily controlled. Owls which had been kept long in the dark were tested with a very weak light from a small opening. The strength of the pupil-motor reaction was as follows: YG, G, GB&B, R&O, BR. For the two investigators the order was: YG, GB, B, O, R, BR. The human eye makes a difference between GB and B and between O and R which the animals do not, but the pupil-valence is the same for the two—green is the strongest color. For the bright adapted human eye the order was G, YB, O, R, BR, B, GB. In the change from brightness to darkness the colors O, R, and BR became darker than the GB and B (Purkinje's phenomenon). The results for the bright adapted eyes of the owls were exactly the same as for man, therefore owl's eyes do undergo adaptation in such conditions and also show the Purkinje phenomenon. Changes in strength of light, a series of 16, showed that in owls there was a real increase in pupil-motor excitability in dark adaptation, inasmuch as the absolute threshhold of the stimulus lay much lower. The human eye under such conditions showed a sensitivity not much greater than in the owl. The results of this investigation agree with those of Hess who showed that cones under daylight vision function similarly to the rods. The dark adaptation experiments showed that the difference between rod seeing and cone seeing is not so great as has previously been supposed.

Leplat (34), in a histological study of the eyes of birds, including nocturnal birds, confirms and corroborates the conclusions of Hess as to their power of accommodation.

AUDITION

Mammals. Part I of Johnson's monograph (29) is concerned with the discrimination of pitch in dogs. He gives a critical historical account of the Pawlow method and of the work of Goltz, Merk, Kalischer, Rothman and Swift. The purpose of Johnson's experiments was to try to confirm Kalischer's results under stricter control and to find a method of testing the power of pitch discrimination in higher vertebrates. In the preliminary experiments, two dogs seemed to have perfected a discrimination between two tones c(256dv) and g(384dv) when sounded on a tuning fork struck by hand, when sounded on the Stern variator, when sounded on forks and different variators indifferently and when included in chords. In response to the low tone, the dogs put their forefeet on a chair and waited to be fed; to the higher tone they were trained to mount a low box for the feeding. It was felt, however, that the control had not been sufficient, that the animals might have been reacting to unconscious cues on the part of the experimenter, who was always in the room, or that they had learned the order of presentation which was not always recorded. For these reasons it was determined to repeat the work under conditions which would render such helps impossible. In the next experiment there was an attempt to train two dogs to react to the same stimulus tones; but in this case the forks were actuated in an adjoining room and the sound was conveyed by tubes to a point just over the animal's cage. The experimenter, in another room, released the cage door by means of a string. The dogs were to respond to the "c" fork by mounting a chair on the west side of the room and to the "e" fork by mounting one on the east side. In case of a proper choice, food was dropped in the chair from a chute above it. After 37 days when each dog had had 505 trials, there was little evidence of discrimination and the conclusion was forced that the first learning had probably been due to unconscious helps, to differences in the duration or intensity of the stimuli, or to some positive habits of the animals. In the next experiment these factors were most carefully watched. The details of the control are given in the monograph. There was a well planned bit of apparatus used which was so arranged that the animals were to go down an alley, and then turn to the right or the left in response to a signal which was not given until they reached the place of turning. It was hoped in this way to overcome the difficulties involved in a delayed reaction. But here again after 92 days the problem was not learned. The contention is faced that a pure tone is too difficult of localization and is too far removed from the tones to which the animal gives instinctive reaction to serve as a useful stimulus for learning. In some later experimentation the animals learned in a few days to localize sounds given by buzzers but the experimentation failed to show that the animals were at all sensitive to pitch differences.

Birds. Lashley (32), from some brief work with an Amazonian parrot, tells us that it imitated singing tones from violin, cello, piano and voice, and that 30 whistling tones were imitated. The register for the singing tones was one octave upward from c 256, for whistling tones two octaves upward from f 384. The response in case of the singing tones was a series of tones with many changes in pitch. The whistling tones were a series of half tones beginning with f 384 and they gave a coefficient of correlation with the stimulus of .658±.059—a correlation far too great to be due to chance alone.

OLFACTION AND CHEMICAL SENSE

Fish. Copeland (12) concludes after a study of the Puffer that while sight plays an important part in the finding of food the reactions to concealed food depend upon olfaction. The experiments with concealed packages of food and cheese cloth showed more visits to the one than to the other and that these reactions depended upon the olfactory organs since they ceased when the sense was rendered inoperative and were only resumed when it again became functional.

Shelford (50, 51) reports some work on the reaction of fish to evaporation and to atmospheric gases. He finds that " short exposure to high evaporation increases the sensibility to high evaporation " and that "in survival time experiments, heightened sensibility was sometimes followed by depression and apparent fatigue." The fish detected differences in the character of the water charged with gases as was shown by definite behavior. The exact mode of detection was not studied.

Parker (43) gives, in the paper here reported, some of the results of his study of *Ammocoetes* and *Amiurus* nebulosus. He is chiefly concerned with the relation of the general chemical sense to taste. He tested the whole body of his animals with different chemicals and gives the exact details of his findings. Like Sheldon he found no stimulating effects from sugar. He thinks sensitivity to sugar is probably a recent evolutionary acquisition and says that it cannot be due to osmotic pressure which is relatively high, but it is a real chemical effect on the nerve endings. There was a considerable diversity in the reactions to quinine and the salt was least efficient except in the mouth. Olfaction is a chemical sense, stimulated in this case by substances in solution. It acts as a distance receptor and is both structurally and functionally in strong contrast to taste. He agrees with Sheldon and Herrick that the chemical sense is the primitive sense from which olfaction and taste have differentiated and attempts to give some of the mechanism of the change.

Amphibians. Copeland (13) from his study of the spotted newt draws conclusions which differ somewhat from those of Reese in 1912. He used the method Parker, Sheldon and others have used and as controls had animals in which the external nares were covered and others in which the olfactory nerves were severed. He thinks there is first a visual response to the object which is then tested as to its food properties by olfaction and that any snapping at an edible object depends upon olfactory stimulation by substances in solution.

Sound as a directing influence in the movement of fishes is the subject of a paper by G. H. Parker (42). The experimenter set up a tank 50 x 6 x 100 cm. made of wood 3.5 cm. thick, with a controllable inlet and outlet for water. The tank was screened and illuminated by reflected light from the ceiling, or from an incandescent light hung directly over it. The stimulus was an iron ball pendulum which struck the exact middle of one end of the tank with a momentum of 361200 C.G.S. units. The ball weighed 4300 gr. The contact produced a low booming noise. Fishes were put in five at a time and tested 50 times. The positions of the fishes in the tank were noted before and after each stimulation. Then the pendulum was shifted to the other end of the tank and the experiment was repeated. The first group of fish was followed by another group of five. *Tautoga*, *Stenotomus*, young kingfish and swellfish, he says, showed unmistakable tendencies to avoid the sound center. Sea robins tended to move toward this center. The killifishes ceased movement but neither moved toward or away from it. He asserts: "It is obvious that fishes are stimulated by sound but most sounds are generated in air and either fail to enter the water or enter it to so slight a degree that they are of little significance for fishes. The surface between the air and the water is an extremely difficult one for sound to penetrate in either direction so that most sounds generated in the water or in the air stay in the medium of their origin. Such sounds as reach fishes, however, not only influence their movements but also the direction of their movements." No doubt all who read Parker's paper will be willing to admit the possibility of the truth of this last statement but few, the reviewer fears, would be willing to admit that he has proved that sound did reach these fish or that their movements were caused by sound.

INSTINCT, HABITS, ETC.

Mammals. Little work with mammals is listed in this field for 1913. Haggerty (24, 25) has published two popular articles. The first deals with some of the methods and results of comparative psychology and the effects of such study upon the development of the science as a whole and the second gives an account of the behavior of apes.

There should be more observational notes on the early development and behavior of animals. Lashley and Watson (33) offer such an account of a young monkey born in the laboratory of Johns Hopkins University. These notes cover a period of 15 weeks. On the sensory side there was noticed what seemed to be slight unadaptive responses to sounds on the second day, some degree of localization was seen by the second week and there was some evidence to show that food was recognized by sight on the fourth week. On the third day the head and eyes followed a moving object and two days later the grasping reflex was seen in connection with an object. The report covers the physical and sensory-motor development, the behavior of the adults toward the young, the play activities and the mode of learning. There was no evidence to show that the young monkey ever gained control over a new activity through imitation.

Franz (16) has an interesting note on the preferential use of the right and left hands by monkeys. The animals used were ones which were being trained previous to certain operations on the occipital lobes. (See Mental Processes of Rhesus Monkeys, *Psy. Rev. Mon.*, Sup. No. 52, 1910.) In the course of this work, some observations were recorded of a series of tests made to discover whether there was any preferential use of either hand. Food, sweet and bitter, was presented on glass plates so that the one was on the right of the animal, the other on the left. The arrangement was carefully changed so that half of the time the sweet was on the right of the animal and half of the time it was on the left. He thinks that more observations are needed before anything definite can be said although the results indicated that of six monkeys one showed a decided preference for the use of the right hand and two preferred the left hand.

Is savageness and wildness inheritable ? This question formed the basis of some experimentation made by Yerkes (59) with rats. The original animals consisted of wild male rats captured in and about Cambridge. The tame rats were taken from a strain bred for ten years past in the Harvard Zoological Laboratory. There were two types of this strain, one of which was known to have more wild blood than the other. These rats were graded from 0 to 5 in savageness, wildness and timidity. The indications of savageness were biting, exposing or gnashing teeth, jumping at hand or forceps and squeaking. The signs of wildness were attempts to hide, excited running, squeaking, urination, defecation. Timidity was indicated by attempts to avoid experimenter, chattering or gnashing of teeth, cowering, urination and defecation. Wild males were crossed with tame females and the offspring, 78 in number, bred by others, were then tested three to five times by the experimenter who did not know the genetic relations of the rat and therefore was entirely unprejudiced. The results showed (a) diminishing savageness, wildness and timidity; (b) sex differences; (c) marked differences from the original stock. Another cross, where the tame female strain had back of it wild blood, showed this wild blood in the first generation. The author thinks the tests prove conclusively that savageness, wildness and timidity are heritable behavior complexes.

Birds. Shepard and Breed (52) compare the relative significance of maturation and use in the development of the pecking instinct of birds. The chicks were incubated absolutely in the dark, taken from the incubator to the dark room at night, fed by hand in the dark for several days, and finally were taken out for experimental observation on the fourth and fifth days. The number of complete pecking reactions in 50 was taken as a standard of accuracy. When brought into the room the chicks were temporarily phototropic. As compared with the normal groups pecking from birth, the points noted were (a) the uniformly poor initial records and (b) the rapidity with which normal accuracy was attained. At the beginning the efficiency of the chicks was 18 per cent below normal but in two day's practice, in which there was no excessive practice due to delay, the birds reached the normal standard. Hence, the experimenters believe, it may be assumed that the curve after the first two days is mainly a curve of maturation.

We have in the article by Craig (14) a continuation of the work reported in 1911 on the stimulation of ovulation in birds, etc. There are 24 new cases given with all of the essential details, where egg laying was brought about by stimulation of other females, by stroking with the hand, by animals in distant cages. He says: " In so far as ovulation is dependent on environment it is dependent, not upon any one afferent stimulus, but upon the entire situation—involving the female's inborn disposition, her whole past history and all the factors in the present environment which affect the social and emotional situation."

On the observational side Sherman (53) gives a careful study of the sparrow hawk. She discusses the nest life and the instinctive activities concerned from the time of choosing the nest to the flight of the fledglings. Bergtold (5) as a result of observations covering six years writes of the distribution, song, food, mating, nests and nestlings of the house finch.

Barrows (4a) relates a curious story of the concealing actions of a bittern. The bittern assumes a characteristic attitude on alighting. Its head, neck and legs are all in the same line and its bill points to the sky. After holding this position for a few minutes it relaxes, draws down its head and seeks for food. Mr. Barrows had the interesting experience of seeing a bittern in this rigid attitude. But the bird, when the cattail flags in which it stood were swayed by a passing breeze, set up a similar motion. The movement involved the whole body even the legs. The observation was repeated and was confirmed by another man.

There are a few articles on bird migration. Phillips (44) treats the subject from the standpoint of its periodic accuracy. He gives facts and figures for a number of birds. For instance, there are records of the return of the bobolink to Concord, Mass., which cover a period of ten years. For this time the average date is May 6 and the greatest deviation from this date only six days. The journey which these birds take, he says, is 2000 miles in length and occupies two months, yet the average error is only 9 per cent. The time of the return of the chimney swifts has been kept in New Market, Va., for twenty-three years. The average error is only 2.2 per cent. The author discusses in a brief way the prevalent theories of migration: (a) the biological theory of distribution; (b) the theory which makes migration a continuous movement and not a single flight due to a migratory impulse; (c) the theory which makes the breeding of tropical birds furnish the impulse for the northern migration of others or which makes it due to the pressure of numbers because of breeding and the consequent lack of food in the dry season; and (d) the sexual hormone theory. The article closes with the following sentence.: "The writer is familiar only in a general way with the subject in hand and has merely attempted to call attention to an aspect of migration which does not appear to have been much discussed."

Cooke (11) deals with the same subject, discussing the relation of weather to migration. From a series of records, extending in some instances over nine years, he makes a comparison of the times of the arrival of certain birds with the weather records of the same seasons. He is interested not only in the time of the arrival but also in the probable effect of the weather on the entire time of the migration. He tries to find out also whether or not the weather of an entire season influences the periodic flight, *i.e.*, whether a long, cold winter or a prolonged hot summer, either in the locality from which the birds come or to which they go, affects the time of migration. He concludes that the variations in the time of arrival from year to year do not agree with the variations of the season, and that during the spring migration the direction of the wind seems to have little or no effect upon the arrival of the birds.

A study of animal hypnosis is found in Mangold's (39) paper. For his own experiments hens have served chiefly. He gives Verworn's explanation of the phenomenon and cites much experimentation with many animals. He attempts to connect it biologically with that spontaneous immobility often seen in animals, *e.g.*, in the hen before the treading of the cock.

LEARNING

Szymanski (54) in a very carefully controlled series of experiments tried to prove whether sound can serve as a stimulus for movements in a definite direction with cats and dogs. He assumed that Kalischer, Swift, Zeliony and others were right in their assertion that dogs and cats can discriminate tones exactly. The experiments were conducted in a dark chamber in a cellar of the institute. The space used was 9 x 2.7 m. in size and was lighted by an electric light hung from the ceiling directly over the place of experimentation. The floor was covered with linoleum and was washed every day with soap and water. For animals he used three fox terriers and two cats. The arrangement of the food boxes, the mode of release of the animals from the cage, the method of giving the stimulus, are all carefully described in the paper. He endeavored to direct the animals to their food by means of sound. They failed within the limits of the experiment to form the association but did develop definite individual habits of response. In the second part of the research he changed to olfaction as a stimulus with the same animals. The experiment was so arranged as to make use of the habits which the animals had set up in the previous work and to strengthen them. Then the mode of procedure was so altered as to compel a modification or change of these habits. He says in discussing this part of the work that if an animal is put in a position where the stimulus is of no particular interest it reacts to this stimulus not directly but with an ordered series of movements. He concludes that his animals were of two types—some more predominantly visual, others kinaesthetic-motor. His experiments were ingenious, his curves and tables are interesting and his discussion is illuminating.

Sackett's work (48) with porcupines, at the Clark University experiment station, was carried on in the summer out of doors, and in the winter in a large unheated room connected with dark dens and an outside runway. There was a strong effort in all of the work to approximate the natural conditions of the animals as far as possible. There were 16 animals in all used in the experimentation.

The paper begins with an interesting account of the natural life of the animal in all phases of its activities.

The first problem undertaken was one connected with right and left-handedness. The results show that porcupines have very little tendency to be either right or left-handed, but that they can be trained in a few days to take food with a given hand. The theories which try to account for right-handedness are discussed at length.

The next task set the animals was to take carrots with one hand and cabbage with the other. After a training covering 5,000 tests, no. 3 reached for cabbage with his right hand no matter when, where, or by whom it was offered. In an interval of 100 days there was little loss of ability. Other animals were used and developed equal skill.

It was not determined upon what sensory basis the above response was made. It may have been olfaction or vision. In some experiments where sweet potato was used instead of cabbage the experimenter thinks that form, size and color were eliminated which leaves brightness as a possible cue. The human element was always present and although the writer concludes "that the animal's basis for reaction was something else than the unconscious idiosyncracies of the experimenter," the reader cannot feel so sure that this was true.

The results from the puzzle box experiments did not differ in any significant way from those obtained by others with different animals.

The third attempt was to teach the animals to discriminate forms. These forms were cut out of wood, and the opening which was to be discriminated was the entrance to the food box. The author says that they learned to discriminate the circle from the other forms when presented in pairs and eventually when given with six others. There was a strong effort to control this part of the work but the basis upon which the choice was made was again left unsettled. The experimenter was always present in these tests.

Color tests, which formed the fourth part of the work, were made by the use of food boxes covered with standard colored papers. They gave negative results.

The brightness tests which followed were more successful. It appeared that the porcupine was able to discriminate a brightness difference of about ten shades of the Nendel series of grays. Observation of the behavior of the animals led to the belief that one animal reacted always by choosing the black while the other reacted by avoiding the white.

In the maze tests the porcupine compared most favorably with other animals. Rotating the maze caused confusion, but they were able to follow the path in the dark when they had learned it in the light and learning in the dark differed little from that in the daylight.

The author says: "Memory tests of the porcupine show better retention where motor or kinaesthetic factors are characteristic of the responses than where the same general motor response follows a choice of sensory stimuli, *i.e.*, ability to thread a maze and operate a puzzle box is retained better than ability to choose between the forms and the brightness boxes."

This paper is suggestive along many lines. The attempt to approach in the experimental field the conditions of nature is one too frequently neglected. One could wish, however, that instead of covering so great a field some of the tests, especially those on the sensory side, could have been carried farther and under stricter control.

McIntyre (35), in a paper before the British Society for the Advancement of Science treated the rôle of memory in animal behavior. The chief questions considered were: the existence of mental images or free ideas in animals, their origin, their biological significance and the tests that indicate their presence.

On the other side of the water the trained horses of Elberfeld have occupied the focal point of attention in the field of animal learning. Nothing seems too abstract, too great or too difficult to attribute to them. The readers of this journal are familiar with the work of Kluge Hans. It is known how his master, von Osten, sincerely believed that the horse could read, spell, etc., how the learned men who visited him were puzzled, and how, finally, under controlled experimentation, it was proved that the horse failed in all questions where the answer was unknown to those present and also when it was impossible for him to see.

Herr von Osten was broken hearted over the outcome but continued his training with the aid of a friend, Herr Krall, who had always remained convinced of the almost human intelligence of the animal. To this friend Herr von Osten left the horse at his death. Krall not only continued Hans's " education " but has also acquired six horses of his own all of which are in training. Some of these far exceed Hans in their attainments.

Krall is a man of intelligence and enthusiasm. He is said to be a good man incapable of dishonesty and for years he has made his home a laboratory for these animals. He is interested in psychology and possesses a considerable psychological library.

Many of the greatest savants in Europe have flocked to see these horses and have made their reports to various societies and in many articles. The account given here is a summary of the facts and no attempt will be made to separate, in the review, the different articles which are listed in the bibliography. The readers are referred especially to Krall's own book and to the articles of Claparède, Buttel-Reepen, and Menegaux for other details.

Krall, after acquiring the horses, tested their visual acuity and range of vision, their perception of color, form, odor, taste, touch, two-point sensitivity, etc., and in each of these graded the horses excellent. The details of this testing are not clear but at least it was attempted. He has tried to give them, and he thinks that they have, ideas of beauty, time, direction, magnetism, etc. He has made an effort to teach them an articulate language. They are said to be able to extract roots to the seventh power, solve problems in algebra, read by taps of the foot, spell phonetically, recognize and name objects and answer questions.

Herr Krall stands before a blackboard and asks the questions orally or writes them on the board, or indicates the letters or figures desired, and the horse upon a special board paws the answer. The groom is usually in the box stall which opens into the room and although the spectators cannot see him it is often possible that the horse can. No one seems to have any suspicion of Herr Krall, but the groom, Albert, is frequently mentioned with doubt.

The vision of some of these horses has been so effectually shut off that there appears to be a general belief that this sensory control has been in some test cases excluded. There is also a blind horse, Barto. If sensory cues are being given here they have failed of discovery since Krall refuses to submit to a commission.

The most remarkable work of the horses is arithmetical. Muhammed solves problems like the following:

$\sqrt[4]{4477456}$ Ans. f., r., 46, repeated, f., f., r. 46.

$\sqrt[2]{4096}$ Ans. f. 36, f. 74, f. 46, f. 46, r. 64.

$$\frac{(3 \times 4) + 36}{3} = ?$$

The following is one of the arrangements which Krall has for use:

7	1	5	4	6
DB	G	R	B	BB

Here are some directions for the use of the diagram:—

Multiply the two right hand numbers. r. 24. Add them. r. 10.

Multiply DB and BB. r. 42. Multiply DB and R. f. 42, f. 34, r. 35.

He sometimes writes the directions on the board as: "Adire vängt troa + dus." Ans. f., f., r. 35.

Phonetic spelling, which Krall says was acquired spontaneously, is strongly urged as a proof of intelligence. That this varies as between horses is also argued as speaking against training. For instance the spelling of the word horse varies in Muhammed and Zariff and each at different times have spelled it as follows:—

Muhammed—bfert, bfrt, färd, färt, fert, frt, faärt, faerd. faert, färb, fpferd, frrt, pärd, pfärt, ppverd, pfer, pferd, tfert, fed, etc.

Zariff—bferd, färed, fferwt, fvert, pfrde, sdfert, pfert, bffet, fdaerp.

In the discussion of Claparède's articles before the French society of Philosophy the arguments as to the intelligence of these horses were clearly stated. Claparède was asked if he thought the fact that the horses had different alphabets was a proof of originality—a proof against the training hypothesis. He was asked whether the obscurity in which the tests were frequently made would not favor signs of some kind provided there was any trickery. Some one else wanted to know how he accounted for the tapping which frequently went on indefinitely. Does the horse ever rectify a mistake was one question. Claparède, to this, replied that he had never seen a mistake rectified by a horse unless there were signs on the part of some one present although Krall said they sometimes did correct their answers voluntarily. Why will not Krall submit to a committee asked one ? Claparède answered " Krall will not put his horses at the entire disposition of a commission because a commission by its nature would alter the character of the responses, introduce new factors, and suppress under the pretense of control the very elements essential for the response." Buttel-Reepen had said that he never saw any spontaneous work of any kind. Claparède was asked here if he ever saw any. He said perhaps the changing from one foot to the other which the animals did in counting units and tens was spontaneous.

The society discussed the mathematical features at some length. It was emphasized that it was impossible for an animal to get at the results in the time which it took them by any of the ordinary operations of arithmetic. They exceeded in ability the finest mathematicians. Krall never would show any of the steps of the work. A man would take years to acquire this ability. How was the horse trained. Mathematicians say that a brain that can extract the fifth root of 147,008,443, should know that even numbers have even roots and that the fourth power of 10,000 cannot be 2. There seems to be a general feeling that the errors do not increase with the difficulty of the problem. M. Plate, however, who took a stenographer with him on his visit says that in his records they did so increase. Claparède's request for simple problems was refused. Some thought that this was because mistakes in very difficult problems would be excused while errors in a simple problem would not be. But the general feeling was that if Herr Krall insisted that this was an intelligent process comparable with that of men he should show its mechanism.

A German protest against the assumptions of Krall was made at the International Congress of Zoology at Monaco. It was signed by Bethe, Bühler, Dorflein, Ettlinger, Forel, Freund, Lippman, Semon, Wundt, Tschermak, Wasmann, and others. They say that the doctrines of Krall and his adherents contradict the conceptions of evolution and are irreconcilable with the facts established by scientific physiology of the senses and by experimental and animal psychology: that such movements will serve to discredit any careful work in animal psychology; that the facts are considered by the undersigned as not proven and improbable; that the conditions do not answer to those of modern psychology, zoology or the methods of the psychology of the senses; and that a profitable discussion is not possible unless the experimental work can be scientifically controlled.

Claparède tries to refute these statements and says that the method of protestation is not a scientific method. He insists that he witnessed tests where correct responses were given under conditions which absolutely excluded the possibility of guidance by voluntary or involuntary signals. But Claparède did not succeed in getting correct answers under conditions where the answer was unknown to those present and Edinger affirms that in his presence any attempt in which the solution was unknown to the attendant did not succeed.

What has been said of the horses applied equally well to the Mannheim dog of which Mackenzie writes and to the horse reported by O'Shea.

The presence or absence of ideas in animals always furnishes a fruitful field for discussion. In the beginning of his monograph on the delayed reaction, Hunter (28a) examines the different lines of evidence offered to prove the presence of such ideas. He then defends the thesis, by means of arguments backed by his experimental investigation, that no ideas need be postulated in a sensory-motor act where the stimulus is present at the moment of the response and that when the brief stimulus and response are separated by an interval the "carrying over" may be by other means than ideas.

Rats, dogs, raccoons and children were trained to go in a definite, though variable, direction, which was indicated by a light previously exposed at the place. The time between the exposure of the light and the release of the subject was then increased as far as possible without destroying the habit. It was found that the maximum delay consistent with a successful response in rats was only 10 sec., in dogs 5 min., in raccoons 25 sec. and in children 25 min. The delay of a child of two and one-half years, however, was less than 1 min. The great significance of the work was not so much in the length of this interval as in the behavior during the interval. The rats were enabled to overcome the delay by preserving a definite orienting attitude of the whole body and the dogs by overt orientation of the head. The raccoons and children maintained no such attitudes. In their cases the author, to account for the successful reactions, assumes that some intra-organic non-orienting representative factor must exist. Thus the reaction cue for all the reagents except the older children is thought to be sensory rather than imaginal and the non-orienting sensory factors are believed to have a memory function which is designated here as sensory thought. This type of mental control, the author reasons, is probably earlier than imaginal thought. The monograph is a valuable one for which a brief review is inadequate.

REFERENCES

1. Assagioli, R. I cavalli pensanti e i lovo critici. *Psiche,* **2,** 349-372.
2. Babak, E. Ueber den Farbensinn des Frosches vermittels Atemreaktion untersucht. *Zeit. f. Sinnesphysiol.,* **47,** 331-351.
3. Baldasseroni, V. Due bestie intelligenti. *Psiche,* **2,** 390-392.
4. Bingham, H. C. Size and Form Perception in Gallus domestica. *Jour. Animal Behav.,* **3,** 65-113.

4aBarrows, W. B. Concealing Actions of the Bittern *Bautaurus Lentiginosus.* The Auk, **30,** 187-190

5. Bergtold, W. H. A Study of the House Finch. *The Auk,* **30,** 40-73.
6. Buttel-Reepen, v. Meine Erfahrung mit den "denkenden" Pferden. *Naturwiss. Woch.,* **28,** 241-245, 257-263.
7. Claparede, E. Les chevaux savants d'Elberfeld. *Archiv. de Psychol.,* **12,** 263-304.
8. Claparede, E. Les chevaux savants d'Elberfeld. *Bull. soc. franc. de Phil.,* **13,** 115-134.
9. Claparede, E. Encore les chevaux d'Elberfeld. *Archv. de Psychol.,* **13,** 244-284.
10. Claparede, E. De tankande hastorna i d'Elberfeld. (Trans.) *Psyke,* **8,** 18-59.
11. Cooke, W. W. The Relation of Bird Migration to the Weather. *The Auk.* **38,** 205-221.
12. Copeland, M. The Olfactory Reactions of the Puffer or Swellfish, *Spheroides Maculatus. Jour. Exper. Zool.,* **12,** 263-268.
13. Copeland, M. The Olfactory Reactions of the Spotted Newt. *Jour. Animal Behav.,* **3,** 260-273.
14. Craig, Wallace. The Stimulation and the Inhibition of Ovulation in Birds. *Jour. Animal Behav.,* **3,** 215-221.
15. Ettinger, M. Der streit um die rechnenden Pferd. (Vortr.) (Samml. *Natur und Kultur* 6), München: *Verl. Natur und Kultur,* S. 54.
16. Franz, S. I. Observations on the Preferential Use of the Right and Left Hands by Monkeys. *Jour. Animal Behav.,* **3,** 140-144.
17. Frisch, K. v. Ueber farbige Anpassung bei Fischen. *Zool. Jahrb., Abt. f allg. Zool. u. Physiol. d. Tiere,* **32,** 171-230.
18. Frisch, K. v. Ueber die Farbenanpassung des Crenilabrus. *Zool. Jahrb., Abt. f. allg. Zool. u. Physiol. d. Tiere,* **33,** 150-164.
19. Frisch, K. v. Sind die Fische Farbenblind? *Zool. Jahrb., Abt. f. allg. Zool. u. Physiol. d. Tiere,* **33,** 107-126.
20. Frisch, K. v. Färbung und Farbensinn der Tiere. *Sitzber. d. Gesell. f. Morph. u. Physiol., Munch.,* **28,** 30-38.
21. Frisch, K. v. Weitere Untersuchungen über den Farbensinn der Fische. *Zool. Jahrb., Abt. f. allg. Zool. u. Physiol. d. Tiere,* **34,** 43-86.
22. Gregg, F. M. and McPheeters, C. A. Behavior of Raccoons to a Temporal Series of Stimuli. *Jour. Animal Behav.,* **3,** 241-259.

23. Haenel, H. Zum Problem der Elberfelder Pferde. *Zeit. f. angew. Psychol.*, **7**, 530-546.
24. Haggerty, M. E. Plumbing the Minds of Apes. *McClure's Mag.*, **41**, 151-154.
25. Haggerty, M. E. Upon the Threshhold of the Mind. *Atlantic Mo.*, **112**, 245-253.
26. Hess, C. Untersuchungen zur Frage nach dem Vorkommen von Farbensinn bei Fischen. *Zool. Jahrb., Abt. f. allg. Zool. u. Physiol. d. Tiere*, **31**, 629-646.
27. Hess, C. Neue Untersuchungen zur vergleichenden Physiologie des Gesichtsinnes. *Zool. Jahrb., Abt. f. allg. Zool. u. Physiol. d. Tiere*, **33**, 387-440.
28. Hunter, W. S. The Question of Form Perception. *Jour. Animal Behav.*, **3**, 329-333.
28aHunter, W. S. The Delayed Reaction in Animals and Children. *Animal Behav. Mon.* **2**, no. 6.
29. Johnson, H. M. Audition and Habit Formation in the Dog. *Animal Behav. Mon.*, **2**, no. 8.
30. Katz, D. and Revesz, G. Ein Beitrag zur Kenntniss des Lichtsinn der Nachtvögel. *Zeit. f. Sinnesphysiol. d. Sinnesorgane*, II, *Abt.* **48**, 165-000.
31. Krall, K. Tänkande djur. (Palme, O., trans.) Upsala: Appleberg, pp. v+295.
32. Lashley, K. S. Reproduction of Inarticulate Sounds in the Parrot. *Jour. Animal Behav.*, **3**, 361-366.
33. Lashley, K. S. and Watson, J. B. Notes on the Development of a Young Monkey. *Jour. Animal Behav.*, **3**, 114-139.
34. Leplat, G. Contribution de l'accommodation chez les oiseaux. *Ann. d'oculistique*, 148, 404-000.
35. McIntyre, J. L. The Rôle of Memory in Animal Behavior. *Rep. Brit. Asso. Adv. Sci.*, **82**, 659-000.
36. Mackenzie, W., Larguier des Bancels, J. and Claparede, E. Le probleme du chien pensant de Mannheim. *Arch. de Psychol.*, **13**, 312-376.
37. Mackenzie, W. Nuove rivelazioni della psiche animale: Il cane "ragionante" di Mannheim. *Psiche*, **2**, 281-348.
38. Mangin, M. Pour l'hypothèse télépathique dans le problème des chevaux d'Elberfeld. *Ann. d. sci. psy.*, **23**, 182-185.
39. Mangold, E. Zur tiereschen Hypnose. *Pfluegers Archiv, f. d. ges. Physiol.*, **150**, 46-57.
40. Menegaux, M. A. L'Education des chevaux pensants D'Elberfeld. *Bull. l'Institute Générale Psychologique*, **13**, 111-158.
41. O'Shea, M. V. The Abilities of an "Educated" Horse. *Pop. Sci. Mo.*, **82**, 168-176.
42. Parker, G. H. Sound as a Directing Influence in the Movement of Fishes. *Bull. U. S. Bureau of Fisheries*, **30**, 99-104.
43. Parker, G. H. The Relation of Smell, Taste and Common Chemical Sense in Vertebrates. *Phil. Acad.*
44. Phillips, J. E. Bird Migration from the Standpoint of its Periodic Accuracy *The Auk*, **38**.
45. Plate, L. Beobachtungen an den denkenden Pferden des Herr Krall. *Naturwiss. Woch.*, **28**, 263-269.
46. Reese, A. M. Food and Chemical Reactions of the Spotted Newt, *Diemyctylus viridescens*. *Jour. Animal Behav.*, **2**, 190-208.
47. Riley, C. F. C. Responses of Young Toads to Light and Contact. *Jour. Animal Behav.*, **3**, 179-214.
48. Sackett, L. W. The Canada Porcupine: A Study of the Learning Process. *Animal Behav. Mon.*, **2**.
49. Schneider, K. C. and Schwantke, C. Die rechende Pferde. *Biol. Centbl.*, **33**, 170-179, 423-425.
50. Shelford, V. E. and Allee, W. C. The Reaction of Fishes to Gradients of Dissolved Atmospheric Gases. *Jour. Exper. Zool.*, **14**, 207-266.
51. Shelford, V. E. The Relation of Certain Animals to Gradients of Evaporating Power of Air. A Study in Experimental Ecology. *Biol. Bull.*, **79-214**.

52. Shepard, J. F. and Breed, F. S. Maturation and Use in the Development of an Instinct. *Jour. Animal Behav.*, **3**, 274-285.
53. Sherman, Althea R. The Nest Life of the Sparrow Hawk. *The Auk*, **30**, 406-418.
54. Szymanski, J. S. Lernversuche bei Hunden und Katzen. *Pfluegers Arch. f. d. ges. Physiol.*, **152**, 307-338.
55. Thompson, J. A. The "Thinking" Horses of Elberfeld. *Contemp. Rev.*, **104**, 799-805.
56. Vesme, C. de. Les chevaux pensants d'Elberfeld. *Ann. d. sci. psych.*, **23**, 117-128, 353-363.
57. Watson, J. B. and Watson, M. I. A study of the Responses of Rodents to Monochromatic Light. *Jour. Animal Behav.*, **3**, 1-14.
58. Wigge, C. Das Problem der Krallschen Pferde. (Kritische Beobachtungen.) Düsseldorf: Schmitz und Olbertz, pp. 23.
59. Yerkes, R. M. Heredity of Savageness and Wildness in Rats. *Jour. Animal Behav.*, **3**, 286-302.

PYCRAFT ON THE INFANCY AND COURTSHIP OF ANIMALS[1]

WALTER S. HUNTER
The University of Texas

In the two volumes here under consideration, Pycraft has presented a large compilation of data bearing upon the two subjects involved. The emphasis throughout is upon the evidences of evolution. The point of view is that of the naturalist and zoologist rather than that of the experimental behaviorist.

The chapter headings lean to the fanciful. The topics covered in the treatise on infancy may be given, however, as follows: Mammals, their coloration, their early activities and the mile-stones of evolution which they present. This is followed by three similar chapters on birds, and these by three more considering the same topics in reptiles. A chapter to each of the following topics completes the book: Tadpoles, the infancy of fishes, the infancy of crabs and caterpillars, and puzzles and paradoxes. The dominant note of this volume is that infancy contains the key to the solution of many important problems of evolution. This is especially emphasized with relation to coloration in the successive change from stripes to spots and then to uniform color. The skeleton, as usual, is made to bear its share of the proof of evolution.

From the standpoint of the readers of this journal, the following points alone need to be made: (1) There is an ever present tendency toward the uncritical acceptance of field observations. On page 25, *e.g.*, we read: "But the finishing touches of this education [play] do certainly seem to be imparted by direct instruction from the parents. Cats certainly train their young in the art of mouse-killing, etc." This, of course, is not borne out by the careful work of Yerkes and Bloomfield.

---

[1] Pycraft, W. P. The Infancy of Animals. Henry Holt & Co., New York, 1913, P. 272.

——— The Courtship of Animals. Henry Holt & Co., New York, 1914, P. 318.

A similar experimental analysis of other cases of instruction and imitation would probably lead to similar results. (2) In discussing the relation of protective coloration to habitat, the author presents the view that the liveries have been evolved to fit the instincts which keep the animals within their peculiar environments. The familiar contrast between the tiger and the lion is a case in point. Inasmuch as the young lion shows traces of a spotted livery, it is to be inferred that at one time the lion wore a striped coat. The evolution to a stage of self-color has followed a change of habitat. Certainly the reverse should be considered, *viz.*, that the instincts may have been forced into alignment with the changes in coloration by the powers of natural selection. (3) The present volume contains a very valuable collection of observations upon instincts. The experimental behaviorists may well take these into account in governing the conditions of their experimentation not only upon instinct itself, but upon discrimination and the "higher" types of behavior.

The volume on the Courtship of Animals draws data from the life-histories of man, the apes, other mammals, birds, reptiles, amphibia, the fishes and insects. The large array of facts defy either summary or review. It must suffice to state the central theoretical problem of the book, the relation of structure and behavior to the theory of sexual selection. The Darwinian theory, in a modified form, is upheld. The brilliant colors and other secondary sexual characters are not to be viewed as the result of sexual selection but as the result of the stimulating activities of "hormones" or juices from the thyroid, pituitary, suprarenal and primary sexual glands. True behavior insight is manifested in regarding the mere activities of posture and display, rather than the type and degree of coloration, as the essential excitant for the female, inasmuch as many somber hued individuals perform the same preliminary antics. The displays and postures also are not to be regarded as the result of sexual selection but are to be viewed as the result of the hormones. The antics of courtship serve to arouse sexual excitement to the proper pitch in the female who then abandons herself to the more exciting performer. All force must be laid upon the more intense "mate-hunger" of the male and his desire for the gratification of the impulse.

A comment above made may be repeated here. For the experimental behaviorist, the observations here recorded offer innumerable suggestions toward the careful analysis of instinct. However the behavior data of courtship, as of any other activity, cannot be adequately handled until the facts of sensory discrimination are gathered. Until that time, however, such discussions as the present are both interesting and stimulating.

tiation of the complex qualities into lesser complex qualities. The development of the pecking instinct in the chick foreshadows the larger development. At first the chick will peck at any thing of the proper size. As it grows older, it learns by experience to peck at certain objects only.

A number of telling criticisms can be directed against Volkelt's position as outlined above: (1) His central problem is the *ignis fatuus* of comparative psychology, *viz.*, knowledge of the structure of animal consciousness. The student can only designate certain functions which experimental evidence indicates are present in behavior. It is not even possible to speak definitely of conscious functions; for in any particular case, the processes in question may be neurological only, *i.e.*, sub-liminal to any consciousness that is present. It is for this reason that the term sensory, *e.g.*, is preferable to the term sensation. (2) This difficulty is well illustrated where the author says that the leading moments or aspects of the complex quality determine behavior without themselves being explicit. It is useless to ask whether animal consciousness is unitary or compounded and whether its aspects are clear and distinct. All that one can say is that certain factors in the environment condition a reaction. It is impossible to say whether these are sub-liminal to consciousness, whether they do fuse with and into a complex quality, or whether they form states which are just as discrete as occur in human consciousness. Either hypothesis can account for the facts because from the nature of the case we may never know conditions which will exclude the truth of either. (3) Volkelt makes much use of the notion that an animal's responses are made to the "whole situation." Thorndike is quoted in support. Now it should be pointed out that while this was a justifiable hypothesis at one time, what we need now are experimental analyses of the "whole situation" in order to determine just what are the stimuli to which the animal responds. As a matter of fact, such work has been and is going on in connection with discrimination tests. The results are not accessible at this writing, but they will undoubtedly do much to put our theories of the stimuli determining animal reactions upon a factual basis. It does not follow because animals, through their reactions, probably break up their world into different types of things than ours that therefore their reactions are conditioned by total situations. The problem is one for experimental, not theoretical, solution.

In additon to the above general criticisms, the following detailed ones may be offered: (1) The bees whose homing was hindered by a rotation of the hive were evidently guided largely by kinaesthetic sensory impulses co-ordinated with the old position of the hive. The other cases drawn from the behavior of birds and spiders indicate merely that the differential cues for food are not the same for those animals that they are for the human observer. Because of this the fly, *e.g.*, is no longer "food" for the spider, but is now an "enemy." Wherever conditions change so that habits and instincts can no longer solve the problem, nonadaptive behavior always presents itself. (One could of course argue very strongly that the behavior of the spider in question was adaptive.) (2) I believe there are few American psychologists who would plead guilty to a championship of "dinghaften Konstantenhaltigkeit" as formulated by Volkelt. All we assume is that upon the second presentation of the same stimulus under the same conditions as at first, the same response will occur. The "übliche Ansicht" which Volkelt criticises has much in common with the abstract conception of an idea which critics seem agreed lay at the basis of Thorndike's address on Ideo-motor Activity at the American Psychological Association in 1912. (3) Volkelt makes individual development a process of particularizing an original complex quality, *e.g.*, the growth of the pecking instinct. He should not forget that there are also instincts whose stimuli are at first very limited. The development here is an increase rather than a decrease in the number of stimuli which will arouse the reaction.

MBL/WHOI LIBRARY
WH 195I $